Comparative Spermatology of Chelicerata: Review and Perspective

Gerd ALBERTI

Zoologisches Institut I (Morphologie/Ökologie),
Universität Heidelberg, Im Neuenheimer Feld 230, D-69120 Heidelberg, Germany.

ABSTRACT

Chelicerata have evolved separately from other arthropods since the Early Cambrian and thus provide many peculiarities aside of convergences realized within the framework of the arthropod concept. The present study describes the current knowledge on sperm cells of chelicerates. The most primitive types are found in the primarily marine taxa, in particular within the Xiphosura. Pantopoda have already quite derived sperm cells. In both groups, distinct character deviations are observable between spermatozoa of different taxa. These demonstrate the applicability of comparative spermatology for phylogenetic or systematic considerations. The most drastic modifications of the basic plan of spermatozoal structure are seen in the Arachnida. Representatives of all main taxa have now been studied, and their sperm cells are briefly discussed. In particular those of Araneae (spiders) and Acari (mites and ticks) have been extensively studied. The spider sperm cells are probably most interesting because of the various transport-forms such as encapsulated individual sperm cells (one cell per capsule: cleistospermia), capsules including several or numerous individual sperm cells (coenospermia and so called "spermatophores"), and, probably exceptional in the whole animal kingdom, capsules containing fused, syncytial sperm (synspermia). Acari all have aflagellate sperm of an extremely differing structure, which allowed the successful application of sperm ultrastructure for systematic purposes. In a subgroup of Acari it was possible to correlate alterations in the sperm structure with modifications in the genital systems and sexual behaviour. Thus, an evolutionary concept of sperm development in this taxon is suggested.

RÉSUMÉ

Spermatologie comparée des Chelicerata: synthèse et perspectives

Les Chelicerata ont évolué indépendamment des autres arthropodes depuis le début du Cambrien et donc montrent de nombreuses particularités ainsi que des convergences réalisées dans le cadre du concept des arthropodes. Ce travail décrit l'état actuel de nos connaissances sur les spermatozoïdes des Chélicérates. Les types les plus primitifs sont rencontrés dans les taxons marins de manière primitive, en particulier les Xiphosura. Les Pantopoda ont déjà des spermatozoïdes très dérivés. Dans les deux groupes, des déviations distinctes des caractères sont observées entre les spermatozoïdes de différents taxons. Ceci démontre que la spermatologie comparée peut être employée pour des considérations phylogénétiques ou systématiques. Les modifications les plus marquées du plan structural de base des spermatozoïdes sont rencontrées chez les Arachnida. Des représentants de tous les taxons principaux ont maintenant été étudiés, et leurs spermatozoïdes sont rapidement commentés. En particulier, les spermatozoïdes des Araneae (araignées) et des Acari (acariens, tiques) ont été étudiés de manière exhaustive. Les spermatozoïdes des araignées sont probablement les plus intéressants du fait des formes de transport variées telles que les spermatozoïdes encapsulés individuellement (une cellule par capsule: cléistospermie), des capsules contenant quelques ou de nombreux spermatozoïdes (coenospermie ou prétendus "spermatophores"), et, probablement exceptionnelles au sein du Règne Animal, des capsules contenant des spermatozoïdes fusionnés ou syncytiaux (synspermie). Les Acariens ont tous des spermatozoïdes aflagellés de structures

ALBERTI, G., 1995. — Comparative spermatology of Chelicerata: review and perspective. *In*: JAMIESON, B. G. M., AUSIO, J., & JUSTINE, J.-L. (eds), Advances in Spermatozoal Phylogeny and Taxonomy. *Mém. Mus. natn. Hist. nat.*, **166** : 203-230. Paris ISBN : 2-85653-225-X.

extrêmement différentes, ce qui permet d'utiliser avec succès l'ultrastructure des spermatozoïdes pour la systématique. Dans un sous-groupe des Acariens il a été possible de corréler les altérations de la structure des spermatozoïdes avec des modifications du système génital et du comportement sexuel. De ce fait, on suggère l'existence d'un concept évolutif du développement des spermatozoïdes dans ce taxon.

Spermatozoa of Chelicerata are now well known from the comparative point of view. Several authors have included spermatological characters in their considerations on phylogenetic systematics of Chelicerata [117, 136, 137], comparative spermatology in general [33], on comparative spermatology as a tool in phylogenetic systematics [138], on arthropod phylogeny [32] or on insect spermatology [75]. However, since not earlier than 1987 (Schizomida) [21] sperm cells of all main taxa had been described at least from one representative species, only an incomplete basis was available to these authors. Moreover, the many remarkable peculiarities shown by chelicerate spermatozoa require a separate study. This may stimulate further investigators to focus on spermatology of this interesting, diverse, and ancient group of arthropods, which has evolved separate from the other arthropods since the Early Cambrian [36, 120].

By far, the greatest structural diversity of spermatozoa is shown among the terrestrial and most species-rich Arachnida, which thus will dominate the following review.

OBSERVATIONS AND DISCUSSION

General aspects

Spermatozoa of Chelicerata represent the main categories of sperm structure distinguished today [32, 33, 35, 66, 74, 75].

The primitive sperm among chelicerates is only found in horse-shoe crabs (Xiphosura) [18, 29, 56, 124] and is characteristic of those taxa exhibiting aquatic fertilization (aquasperm) [sensu 74]. This type is classically characterized by a spherical head containing the acrosomal complex and nucleus with condensed chromatin, a middle piece containing a few relatively large mitochondria, and an elongate sperm tail representing the flagellum. The distal centriole is connected by an elaborate anchoring complex to the plasmalemma. It is already distinctly modified, however, in the Xiphosura [1, 18] (Fig. 1). The acrosomal complex is remarkable because of its very long acrosomal filament (perforatorium) which runs through the nucleus and is coiled around it. The chromatin is not as condensed as is usually the case in mature spermatozoa. The number of rather small mitochondria is quite high and a distinct middle piece is not always recognizable since the mitochondria may be scattered throughout the cytoplasm surrounding the nucleus in the spherical head region [18]. There is also no prominent anchoring complex [18, 56] and the axoneme of the flagellum may lack the central tubules (in the Indowest-Pacific species of *Tachypleus* and *Carcinoscorpius*) [18, 147].

The modified (derived) sperm (filiform-flagellate, biflagellate, or aflagellate to mention some obvious deviations from the primitive type) is characteristic of taxa exhibiting a modified fertilization. It is found thus in those aquatic (marine) taxa which have developed internal fertilization or are at least close to it and in terrestrial animals which depend on internal fertilization. Thus, in Chelicerata modified sperm cells are found in the marine Pantopoda and in Arachnida, which are primarily terrestrial animals.

In Pantopoda (Pycnogonida), the sperm of *Nymphon* species are still close to the primitive type (Fig. 1). However, an acrosomal complex is lacking and the nucleus is elongated. It is surrounded by longitudinally arranged microtubules which persist in the mature sperm cell. Similar to xiphosurans, chromatin condensation is only weak. The proximal centriole is reduced. There is a long flagellum in which considerable inter- and intraspecific variation in the axonemal pattern (9+0 to 18+0) occurs [48, 49, 52]. The sperm cells of *Nymphon* are motile. On the contrary, the elongate, immotile spermatozoa of *Pycnogonum littorale* are highly modified and

contain numerous longitudinally arranged microtubules (more than 1000) forming complex patterns. Aside of folded membranes (nuclear derivative?) found in the central part of the cell no further organelles were seen [49].

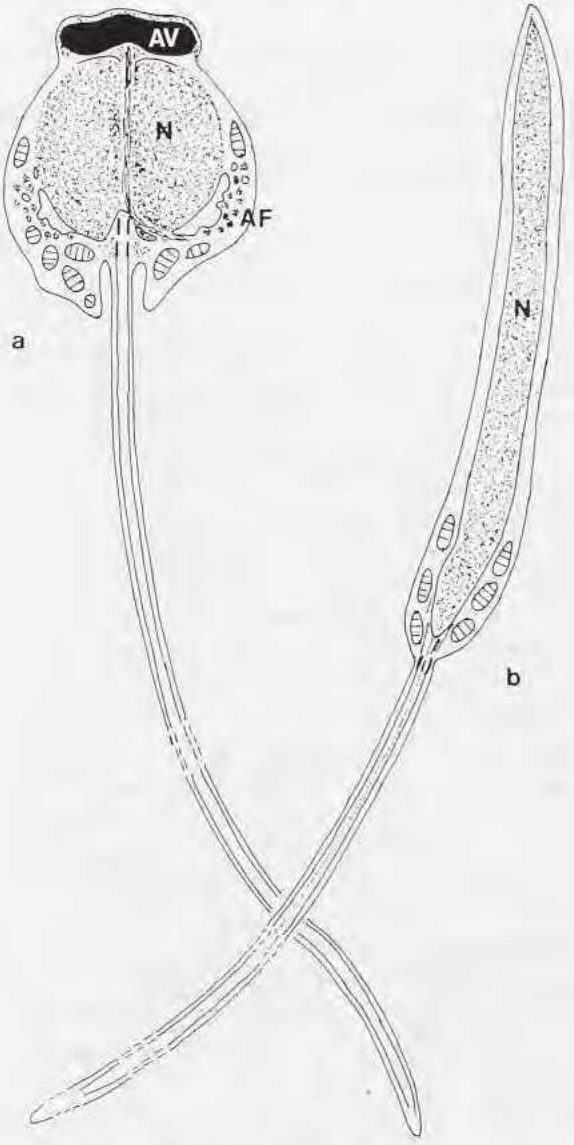


FIG. 1. — Diagrams of sperm of the primary marine chelicerates, Xiphosura and Pantopoda. **a:** *Tachypleus gigas* (Xiphosura) sperm are still close to the primitive type of sperm (aquasperm). The spermatozoon possesses a spherical head, a pronounced acrosomal complex, and a long flagellum. Note characters which deviate from the primitive sperm: very long acrosomal filament penetrating the nucleus and coiling around it, indistinct middle piece. In contrast to *Limulus polyphemus*, this species has a flagellum with 9x2+0 axoneme [18]. **b:** *Nymphon* sp. (Pantopoda). The sperm is further derived. It lacks an acrosomal complex, the head is elongated, the middle piece is indistinct, there is only one centriole [49, 52]. AF, acrosomal filament; AV, acrosomal vacuole; N, nucleus.

In Arachnida the main subtypes of modified sperm cells are distributed through the taxa as follows: filiform-flagellate (Scorpiones), coiled-flagellate (Pseudoscorpiones, Uropygi, Amblypygi, Araneae, Ricinulei), and aflagellate spermatozoa (Opiliones, Palpigradi, Solifugae, Acari) [4-8, 12, 13, 29, 21, 32, 33]. However, this classification gives only a rough impression of the diversity found within Arachnida: any conventional structure of sperm cells may be varied. Fig. 2 gives an impression of the various types of sperm depicting an example of each of the major taxa.

The extraordinary diversity may be first simply expressed by variations in magnitude. Sperm cells of Arachnida range between less than 2 µm (*Nicoletiella lutea*/Acari-Actinotrichida; *Siro duricorius*/Opiliones-Cyphophthalmi) [5, ALBERTI, unpublished] to 1000 µm in the argasid tick *Ornithodorus tholozani* (capacitated sperm cell; see below) [63].

The individual sperm cell may be of a very complex structure (e.g. Pseudoscorpiones; certain Acari-Anactinotrichida; Fig. 2) or may be rather simple (e.g. Solifugae; certain Acari-Actinotrichida) [5, 7] (Fig. 2). In the spider mite *Tetranychus urticae* (Acari-Actinotrichida), spermatozoa merely are comprised of a chromatin body, some cytoplasm, and a plasmalemma with tubular indentations [22].

However, primarily arachnid spermatozoa possess the same set of organelles which characterizes the ground plan of the metazoan sperm cell [33-35] (see above).

BACCETTI [32, 33] several times stressed the major evolutionary alterations in the arachnids: coiling of sperm cells and loss of flagellum.

In the following, modifications of conventional structures will be described at first, and secondly, new types of organization will be considered.

Acrosomal complex

The acrosomal complex typically is composed of an acrosomal vesicle (vacuole) and an acrosomal filament (perforatorium) (Fig. 3). The space between acrosomal vacuole and plasmalemma is occupied by a more or less distinct substance termed preacrosomal (also extraacrosomal or periacrosomal) material. The acrosomal filament is part of the subacrosomal material containing actin filaments which are highly ordered [124]. Another component appears as an amorphous substance and is termed an intermediate substance. This acrosomal complex is primarily present in all arachnid orders, probably with the only exception of Palpigradi, in which no acrosomal filament is found (however, only one species has been observed until now) [4]. Sometimes these conventional structures achieve a peculiar organization. In contrast to certain other scorpions in which the acrosomal complex is at the tip of the elongate nucleus, in the sperm of *Buthus occitanus* the very small acrosomal vacuole is located aside of the helical anterior part of the nucleus. The subacrosomal material (more strictly the intermediate substance) surrounds the whole tip of the nucleus [8], comparable to the subacrosomal cone found in certain Onychophora [74, 75]. A peculiar situation is observable in the opilionid *Nemastoma lugubre* [ALBERTI, unpublished] where subacrosomal material spreads between nuclear envelope and plasmalemma. Thus it apparently connects the latter to the nucleus and moulds the cell parallel to chromatin condensation and nuclear shaping [see also 81]. At the first glance, the situation found in certain Acari-Anactinotrichida (namely in the vacuolated type of sperm) [6, 9, 13] is quite similar as in the opilionid just mentioned. Here the acrosomal vacuole is developed into a flat cisterna growing from a central acrosomal plate [6, 41, 42]. This flat cisterna is connected to the plasmalemma by preacrosomal material and the shape of the cell obviously is influenced by this (Fig. 8e).

The preacrosomal material often contains filaments which are probably stabilizing the anterior region of the cell during the acrosomal reaction [124]. Such filaments were found in several Araneae [24, 26, 109] and in the micro whip scorpion *Schizomus palaciosi* [21] (Fig. 3b). In the latter an intricate paracrosomal lattice structure appears in the late stages of spermiogenesis as a transient structure (Figs 3d, 5). Regarding the various shapes of the acrosomal vacuole one extraordinary example was already demonstrated from the Acari-Anactinotrichida (Figs 2, 8a, c, e). Another well-known example is that of pseudoscorpions. In this group the acrosomal vacuole continues into a spiral band which surrounds the elongate smooth nucleus [40, 133] (Fig. 2). A peculiar sickle-shaped acrosomal vacuole was observed in Ricinulei [20] (Fig. 3c).

Finally it may be mentioned that certain taxa of Opiliones and Acari have lost the acrosomal filament (as *Prokoenenia wheeleri*, Palpigradi) [4] or are completely devoid of an acrosomal complex. Sometimes this occurs in the same genus: *Siro rubens* (Opiliones) with all acrosomal components) [80], *Siro duricorius* without acrosomal complex [ALBERTI, unpublished].

Nucleus

Whereas the corkscrew appearance of the nuclear region in Pseudoscorpiones is derived from the peculiar spiral band (acrosomal vacuole), the nuclei of certain scorpions and of Uropygi themselves exhibit a helical, in Amblypygi and basically also in Araneae a corkscrew shape (with sharp edges) [8, 24, 40, 76, 103, 107, 126, 133, 134] (Fig. 5). In the latter and also in the uropygid *Mastigoproctus giganteus*, the acrosomal filament spirals around the periphery of the nucleus enclosed in a nuclear canal [24, 103, 107] (Figs 3e, 4, 5). In Amblypygi and Araneae there is a tendency toward asymmetry of the nucleus which extends beyond the implantation fossa into a postcentriolar nuclear elongation [12, 26]. This asymmetry may be extremely developed in spiders of the genus *Tetragnatha* (Tetragnathidae) [12], in which the basis of the axoneme comes close to the acrosomal vacuole. On the other hand, the nucleus of *Pholcus phalangioides* (Pholcidae; Araneae) is nearly of radial symmetry, which is a derived characteristic as can be concluded by comparison with related taxa [24] (Fig. 5).

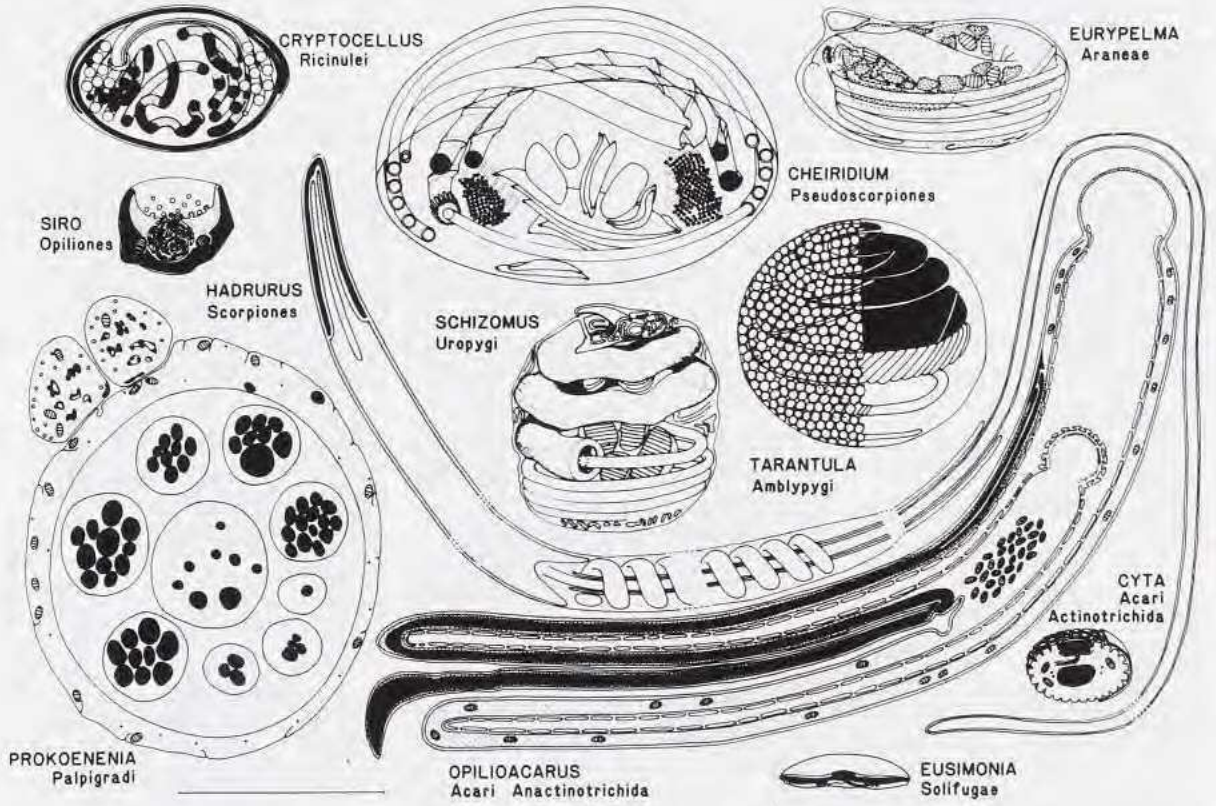


FIG. 2. — Synoptic view of spermatozoa of the terrestrial Arachnida (representatives of some taxa have secondarily invaded limnic and marine habitats). The spermatozoon of the scorpion is drawn in reduced length (full length: 275 µm). Spermatozoa of *Siro duricorius* and *Cheiridium museorum* [original], others [4-7, 9, 21, 26, 76, 77]. *Opilioacarus*: now *Neocarus*. Scale bar: 5 µm.

A comparable tendency as in *Tetragnatha*, probably even more peculiar, is observable in the ricinuleid *Cryptocellus boneti* [20]. In this species the axoneme is directly connected with the acrosomal vacuole, a situation - to the author's knowledge - not found anywhere else. However, the nucleus is not asymmetrical in contrast to *Tetragnatha*, though of extraordinary shape. The anterior part is a thin tube containing the acrosomal filament (Fig. 3c).

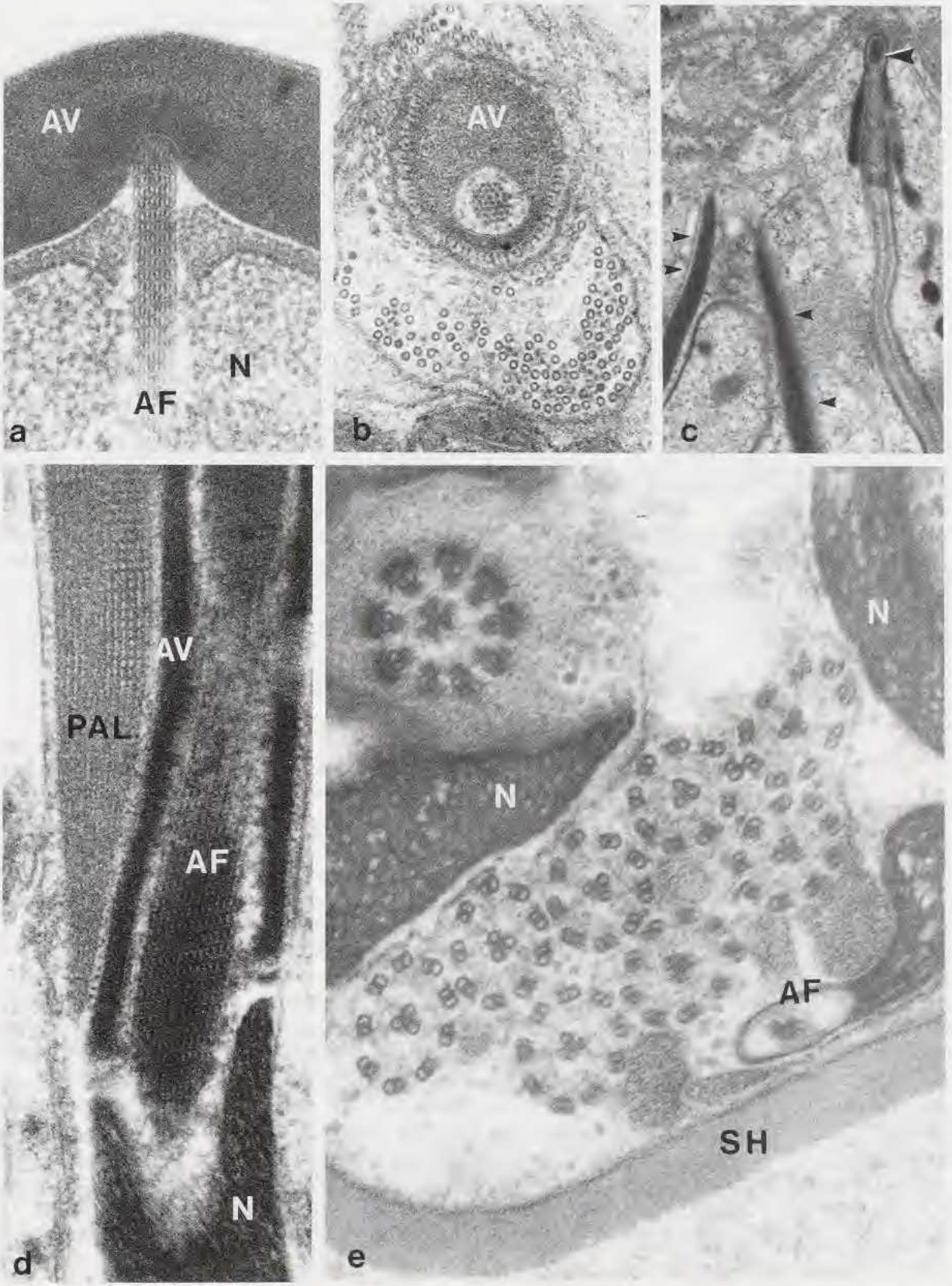
Even though these are only few examples, it is evident, that the nuclei may exhibit a considerable variety of shapes. In the flagellate spermatozoa, whether filiform or coiled, it is basically a large elongate organelle (Scorpiones, Pseudoscorpiones, Uropygi, Amblypygi, Araneae) [8, 20, 21, 76, 77, 103, 107, 126, 133, 134], which may even extend beyond the posterior end of the flagellum (*Cryptocellus boneti*) [20]. It is of interest, also from the viewpoint of functional spermatology, that a manchette of microtubules is observed only in some of these spermatozoa, namely in those of Uropygi, Amblypygi, Araneae and Ricinulei [20, 24, 26, 76, 126]. No manchette is found in Scorpiones and Pseudoscorpiones [40, 72, 77, 106, 133]. At this point it is not intended to continue the discussion on the possible function of a manchette of microtubules in nuclear shaping [see 21, 58, 127 for references]. It may only be mentioned that the microtubules exhibit alterations in their arrangement parallel to nuclear condensation in *Schizomus palaciosi* [21]. They follow exactly the sometimes aberrant configurations of the spermatid nuclei (e.g. in *Tetragnatha*) [12]. The manchette microtubules disappear at the end of spermiogenesis (see the pantopod *Nymphon*, however).

Another characteristic which largely varies within the Arachnida is the implantation fossa, a posterior region of the nucleus which usually contains the centrioles or their derivatives. The fossa may be a shallow, funnel-shaped indentation as in scorpions [8, 77], Uropygi/Thelyphonida [107], Amblypygi [76, 126] and Pseudoscorpiones [40, 134]. On the contrary, in Uropygi/Schizomida and many spiders the implantation fossa is deep, sometimes making the sperm almost a hollow tube (e.g. *Schizomus palaciosi*-Schizomida, *Pholcus phalangioides*-Araneae) [21, 24] (Figs 4, 5). Often dense material occupies the lumen of the fossa. This material may be homogeneous, granular (e.g. *Pholcus*) or may contain filaments or microtubules [92]. Within aflagellate spermatozoa an implantation fossa is observable only in opilionids. This is connected, in the genus *Siro*, with the transient appearance of a flagellum during spermiogenesis and is only a very shallow depression of the nuclear surface [80]. Nevertheless, in other opilionids a deep and broad invagination which contains the centrioles may occur [78, 81, 125].

In the aflagellate spermatozoa elongate, bulky, spherical, disc-, and bowl-shaped nuclei may be encountered (Fig. 2). It appears as if, after giving up the "basic plan" in early times, nearly any possibility of altering the shape of nucleus and cell has been realized. What is remarkable in particular with regard to the nucleus is the disappearance of the nuclear envelope in

---

FIG. 3. — Details of spermatozoa of various Chelicerata. **a:** Acrosomal region of *Tachypleus gigas* (Xiphosura). Note acrosomal filament originating in the centre of a slight posterior indentation of the acrosomal vacuole and showing regularly arranged subfibres (actin) and nucleus with only loosely arranged chromatin [18]. x 53 000. **b:** Late spermatid of *Filistata insidiatrix* (Araneae). The cap-like acrosomal vacuole is sectioned transversely and the acrosomal filament composed of subfibres is shown. The acrosomal vacuole is surrounded by thin filaments. Note manchette microtubules [24]. x 49 500. **c:** Spermatid of *Cryptocellus boneti* (Ricinulei). The small, sickle shaped acrosomal vacuole is sectioned transversely (large arrowhead). It is surrounded by dense streaks. Note axoneme originating immediately behind the acrosomal vacuole (the nucleus lies parallel to the axoneme and is not shown in this figure). At left two of the dense plates which later ensheath the spermatozoon are seen (small arrowheads) (compare Figs. 2 and 5) [20]. x 28 500. **d:** Spermatid of *Schizomus palaciosi* (Uropygi-Schizomida). The basis of the long acrosomal vacuole, which is deeply indented from behind, rests on the nucleus. The acrosomal filament is rather thick and shows the same pattern of subfibres as in *Tachypleus gigas* (compare a). Note the paracrosomal lattice structure, which is only present during a short period in spermiogenesis [21]. x 63 000. **e:** Part of synspermium, i.e. the product of four fused spermatids, of *Segestria senoculata* (Araneae) showing basis of one axoneme and transverse sections through the coils of all four axonemes. Note 9x2 +3 axonemal pattern (synapomorphy of Megoperculata: Uropygi, Amblypygi and Araneae) and the absence of membranes separating the axonemes, what indicates the complete fusion between the four spermatids. A secretion sheath surrounds the synspermium [24]. AF, acrosomal filament; AV, acrosomal vacuole; N, nucleus; PAL, paracrosomal lattice structure; SH, sheath of secretion.



Solifugae and Acari-Actinotrichida at the end of spermiogenesis. In these taxa the acrosomal filament penetrates through the chromatin body and thus directly contacts the cytoplasmic matrix [6, 7] (Figs 6d, 8d). A similar situation is to the author's knowledge found only in Xiphosura [18, 56] (Fig. 1).

Midpiece

Since the work of ANDRÉ [28] the differentiation of the middle piece and chondriome in scorpions is known in detail. This is an example of extensive reorganization of mitochondria into elongate tubular structures (compare Fig. 2). No comparable elongation apparently occurs in Amblypygi and the early derived spider *Heptathela kimurai* (Mesothelae) [103] in which numerous mitochondria are arranged helically. Though quite different, in these three taxa a typical middle piece is established with mitochondria surrounding the flagellum or the axoneme respectively (Figs 4,5). In pseudoscorpions a different situation is found. The mitochondria are very elongate, thin tubular structures which are attached to the basis of the axoneme but they are otherwise situated in the cytoplasm of the coiled spermatozoon (see below) independently from the axoneme, where they establish a mitochondrial ring [40, 125] (Fig. 2). Contrary to scorpions, in pseudoscorpions the mitochondria are attached to the bases of the flagellum by an intricate structure (compare Fig. 2). In Uropygi no middle piece is encountered [21, 107, & PHILLIPS, 1986, pers. com.] (Fig. 5) as is the case in Ricinulei [20]. In Araneae, beside the primitive condition shown in *Heptathela*, mitochondria can be located without special arrangement (e.g. orthognath spiders, several labidognath spiders) [24, 26] or can be completely absent [93, 104] in the mature spermatozoa. Sometimes mitochondria pass through a "primitive" position in spermiogenesis being for some time located at the posterior end of the nucleus close to the basis of the flagellum (*Schizomus palaciosi*, several Araneae) [12, 21] (Fig. 5: *Schizomus*). In the aflagellate spermatozoa mitochondria are found in various positions sometimes "embedded" in the nucleus or chromatin body respectively (in the opilionid genus *Siro* and certain Acari-Actinotrichida) [6, 27, 64, 80, 142] (Fig. 7). Spermatozoa of some taxa may be devoid of mitochondria (e.g. *Tetranychus urticae*/Acari-Actinotrichida) [22].

Axoneme

The flagellum or axoneme respectively, if present, starts with two centrioles (Pantopoda are different in this respect; see above) arranged coaxially, an arrangement also found in the Xiphosura [18, 56] (Fig. 1). Thus this derived characteristic may be regarded as a synapomorphy of the chelicerates [136, 137]. Sometimes, however, the centrioles are arranged nearly orthogonally as in the mature spermatozoa of bird spiders [26]. Spermiogenesis reveals that this position is a derived arrangement in these spiders, probably caused by the coiling process, and follows a phase in which the centrioles are in tandem position. Even the original orthogonal arrangement is observable in the early stages of spermatogenesis [26].

One of the most interesting results from the viewpoint of comparative spermatology in Arachnology was the discovery of the 9x2 +3 axoneme in Araneae [103, 112], Uropygi [21, 107] and Amblypygi [76, 126] demonstrating the close relationship of these taxa with a spermatological criterion (Fig. 3e). However, even this apparently very stable characteristic (compared with the variability found e.g. in scorpions) [8, 72, 77] is altered in certain spiders (Linyphiidae) in which a 9x2 +0 axoneme occurs [12]. Thus this axoneme is by convergence similar to that of the xiphosuran genera *Tachypleus* and *Carcinoscorpius* [18, 147] and several scorpions [72].

Sometimes dense material surrounds the distal centriole thus probably establishing an anchoring complex (*Pholcus phalangioides*, *Dysdera* sp., *Segestria senoculata*; Araneae) [24] (Figs 3e, 6b). In spiders the number of tubules constituting the centrioles may be reduced and/or

dense fibres may be attached to the base of the axoneme. In *Cryptocellus boneti* (Ricinulei) the proximal centriole disappears during late spermiogenesis [20].

The only case where an aflagellate spermatozoon reveals relicts of an axoneme is represented by the cyphophthalmid *Siro* [80]. In these tiny opilionids a flagellate stage is observable during spermiogenesis.

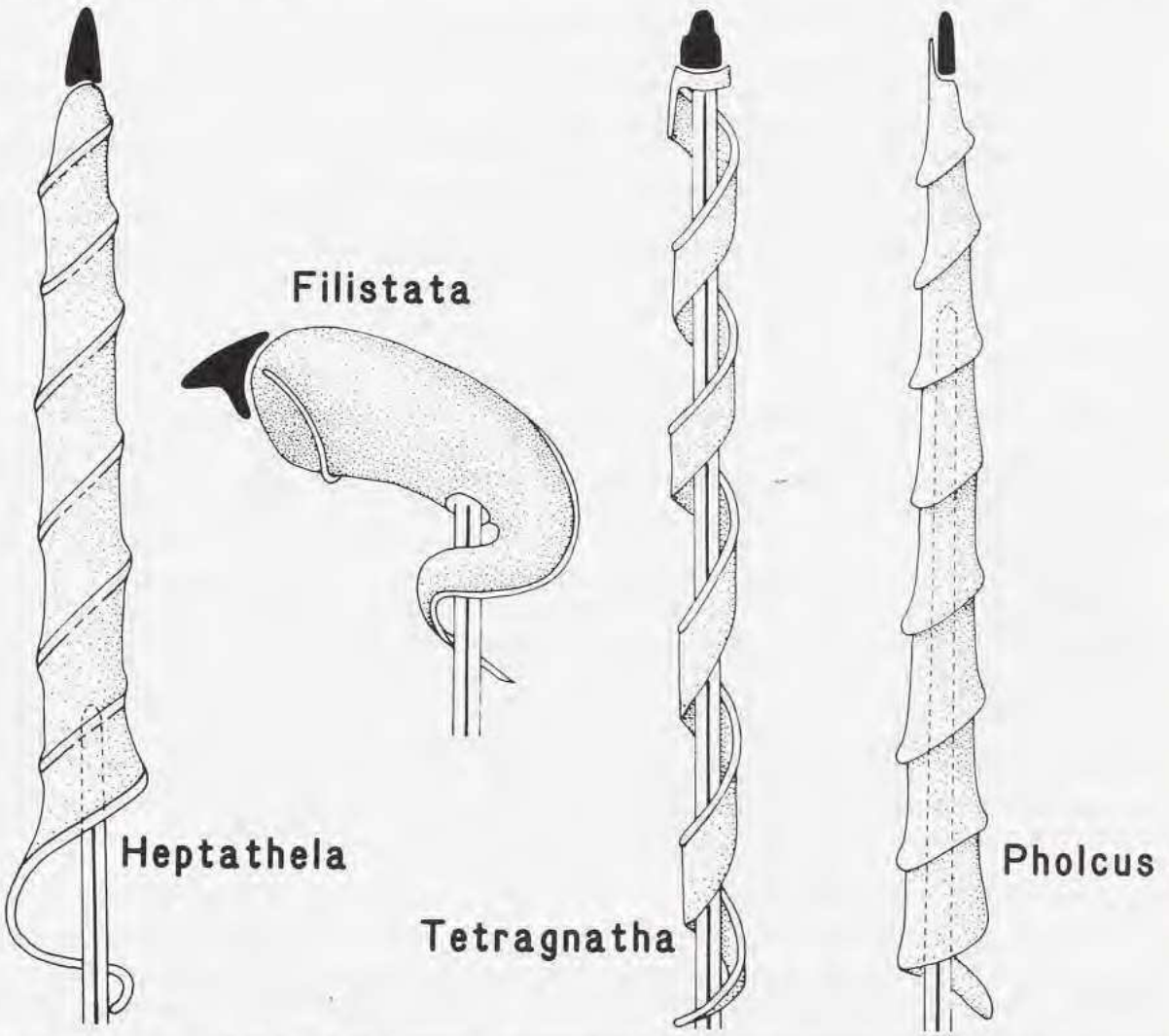


FIG. 4. — Different shapes of nuclei of spermatids of spiders and their relation to acrosomal complex and axoneme. **a:** *Heptathela kimurai* (Liphistiidae, Mesothelae). **b:** *Filistata insidiatrix* (Filistatidae, Opisthothelae). **c:** *Tetragnatha montana* (Tetragnathidae, Opisthothelae). **d:** *Pholcus phalangioides* (Pholcidae, Opisthothelae). The *Filistata*-type is the most common in spiders and may be close to the plesiomorphic type of Opisthothelae [12].

A peculiarity of scorpions and pseudoscorpions is the flagellar tunnel surrounding the axoneme and separating it from the middle piece mitochondria (in scorpions) and from the cytoplasmic matrix respectively (of the coiled cell in the pseudoscorpions) (Fig. 2). Whereas in the scorpions the flagellar tunnel comprises a distinct extracellular space, this is completely absent in pseudoscorpions owing to the close apposition of the membranes, which in early stages had delimited it. In scorpions and in some pseudoscorpions a dense cylinder surrounds the flagellar

tunnel. A flagellar tunnel is also observable during spermiogenesis of Uropygi, Amblypygi, Araneae and Ricinulei but disappears later [20, 21, 76, 107, 125]. Thus the axoneme is not surrounded by its genuine membrane in the mature spermatozoa of these taxa (Figs 3e, 6a, b).

It is important to note that the flagellar tunnel separates the flagellum from the mitochondrial sheath (in scorpions) or mitochondrial ring (in pseudoscorpions). In Amblypygi and the early derived spider *Heptathela*, in which a middle piece is still existent, the flagellar tunnel disappears before the mitochondria occupy their definite position (Fig. 5).

A flagellar tunnel appears also in connection with the transient flagellum of *Siro*. It is retained after the axonemal tubules have been withdrawn as a peculiar "crypt" containing numerous microvilli [80, ALBERTI, unpublished].

The flagellar tunnel may be derived from the cytoplasmic collar around the flagellar basis in xiphosuran sperm. No such structure occurs in Pantopoda (Fig. 1).

In addition to the diversity achieved in arachnids by variations of the basic sperm components "new" structures are introduced into this cell type resulting in new structural and functional possibilities and extraordinary peculiarities. These are dealt with in the following.

Vesiculation and vacuoles

Arachnid spermatozoa are very often rich in vesicles and cisternae, especially those belonging to the coiled-flagellate type. These vesicles - at least partly a result of the coiling process during which surface membranes are likely internalized - may be arranged very regularly under the plasmalemma (Uropygi/Thelyphonida, Amblypygi) [76, 107, 126] (Figs 2, 5). In Araneae and Ricinulei such vesicles and cisternae often contain dense material forming "dense streaks" (Fig. 3c). In certain Araneae vesicles fuse to large vacuoles [24]. In addition to these structures further vesicles are derived by an extended activity of the Golgi apparatus. In Ricinulei dark plates are formed early in spermatogenesis and contribute to an intracellular capsule enclosing the central components of the mature spermatozoon (Figs 2, 3c) [20]. In the palpigrade *Prokoenenia wheeleri* a huge vacuole dominates the large cell, which was previously thought to be a spermatophore (Fig. 2). The spermatozoa of certain Acari/Anactinotrichida develop during a very complex spermatogenesis a conspicuous vacuole bordered by a complex periphery bearing numerous "cellular processes" [5, 42, 63, 131] (Figs 2, 7, 8a,c). Perhaps the pouches of the ribbon sperm of related mites are derived from the vesicular precursors of the large vacuole characterizing the vacuolate type (Figs 8b) [5, 9, 13, 139-141].

Transport forms - sperm aggregates

Another aspect which was newly (or independently from non-arachnids) achieved during the evolution of spermatozoa of Arachnida is the establishment of secondary events. These transform elongate spermatozoa into the already mentioned coiled spermatozoa (Figs 2, 6a, b). In Uropygi and Amblypygi the coiling process starts from the posterior (flagellar) part of the cell resulting in a spherical mature spermatozoon. It is of interest to note that this coiling process is incomplete in the early derived spider *Heptathela kimurai* (Mesothelae) [89, 103]. Only the flagellum and posterior part of the nucleus are involved. In the bird spiders (orthognath spiders) the coiling is more complete, leaving only the acrosomal region projecting slightly from the otherwise more or less spherical cell [26]. Finally, in (most) labidognath spiders the whole cell including the acrosomal region is completely coiled or spherical again [12, 15, 24, 39, 92, 93, 104, 109]. If it is assumed that the spherical shape is the plesiomorphic state within the "Pedipalpi"-Araneae, the spiders demonstrate, probably, a nice example of a round about way in the evolution of their sperm cells. In Araneae the coiled cell is surrounded by an extracellular secretion sheath in different ways (Figs 3e, 6b and see below).

The coiling of the spermatid of Pseudoscorpions is a process which largely takes place in an extensive vacuole [134]. After completion of coiling the vacuole is transformed into smaller vesicles or cisternae (Fig. 2).

Extracellular material or secretions may loosely combine several spermatozoa to form aggregates (Scorpiones, Solifugae, Bdellidae/Acari/Actinotrichida) [7, 8, 10, 23] (Fig. 6c, d). In Opiliones/Cyphophthalmi the aggregates include dimorphic spermatozoa [80, ALBERTI, unpublished] (Fig. 6c). Such sperm aggregations in turn may be surrounded by a common sheath as in spiders of the families Theraphosidae and Filistatidae (coenospermia) [12, 24, 26, 37]. Rarely, such aggregates can deviate from the spherical shape. Thus, in Telemidae an elongate, rather complex tubular "spermatophore" is found [82]. A peculiarity observed to the author's knowledge only in a few Araneae (Dysderidae, Segestriidae, Scytodidae, Sicariidae) is occurence of syncytial spermatozoa (synspermia) [10, 12, 24] (Figs 3e, 6b). This fusion (or incomplete separation of spermatids) occurs already within the testis, whereas the coenospermia and spermatophores (Telemidae) are surrounded by a secretion sheath in the distal vas deferens as is the case in the majority of spiders which encase single sperm cells (cleistospermia) [12, 15, 24].

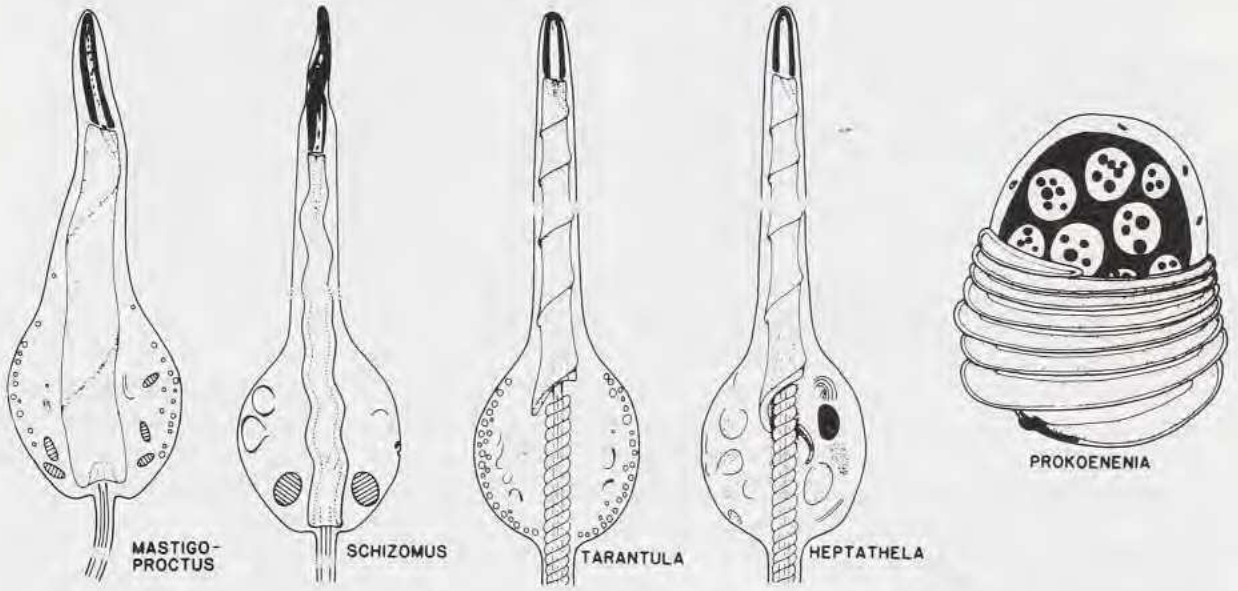


FIG. 5. — Late spermatids of: **a:** *Mastigoproctus giganteus* (Uropygi-Thelyphonida). **b:** *Schizomus palaciosi* (Uropygi-Schizomida). **c:** *Tarantula marginemaculata*. **d:** *Heptathela kimurai* (Araneae-Mesothelae). **e:** *Prokoenenia wheeleri* (Palpigradi). Note that the spermatid of the palpigradid deviates completely from those of the Megoperculata. A synapomorphy of Amblypygi and Araneae may be the postcentriolar elongation of the nucleus. The spermatids of *Schizomus*, *Tarantula* and *Heptathela* are drawn in reduced length [12].

Activation, maturation and capacitation

The spermatozoa of *Limulus polyphemus* remain immotile until they come into contact with a component which is released from the egg layer [44].

Spermatozoa of many taxa undergo certain modifications after leaving the male by which they achieve the capacity to fertilize the oocyte (capacitation) [35]. These transformations may be restricted to the molecular level as in mammals or may involve distinct morphological alterations [102, 130]. It is evident that these processes have to occur in a taxon-specific way since the sperm cells have to cope with a specific environment. In terrestrial animals this is usually the female genital tract. Exceptions are species with dermal insemination such as some Onychophora [94,

118, 119] in which the sperm cells migrate through the body cavity. In many arachnids the mentioned transformations occur in a rather drastic way. However, these events are poorly investigated. The transport form in which the sperm is transferred to the female is changed into the fertile, active sperm.

From Araneae and Pseudoscorpions it is known that spermatozoa uncoil in the female [37, 40] and only then are fertile [45]. Probably these events are facilitated by the mentioned vesicles and vacuoles which may be integrated into the plasmalemma when elongation of the cell occurs. This process is well known and very intricate in the vacuolated sperm cells of ticks and some mites (Acari/Anactinotrichida). The shape of the cell is completely changed by a turning-inside-out-process which brings the cellular processes to the surface of the cell [13, 41, 42, 63, 101, 113, 131]. After that, the sperm cells are capable of several kinds of motion [60, 101] (see Figs 2, 7, 8a, c for cells prior to capacitation).

In ticks, and probably also in anactinotrichid mites with vacuolate spermatozoa, a further transformation of the cell occurs prior to insemination. A posterior portion of the sperm cell which is invaginated into the cytoplasmic column (inner core), forming a so-called acrosomal canal in several species, is also evaginated and contains the nucleus [63, 113]. It has been suggested that only this nucleus-containing part of the capacitated spermatozoon enters the oocyte [101, 113].

In the ribbon spermatozoa of a related mite, *Varroa jacobsoni*, the spherical cell transforms into an elongate cell with completely new appearance and structures which are probably related to the achievement of motility [17].

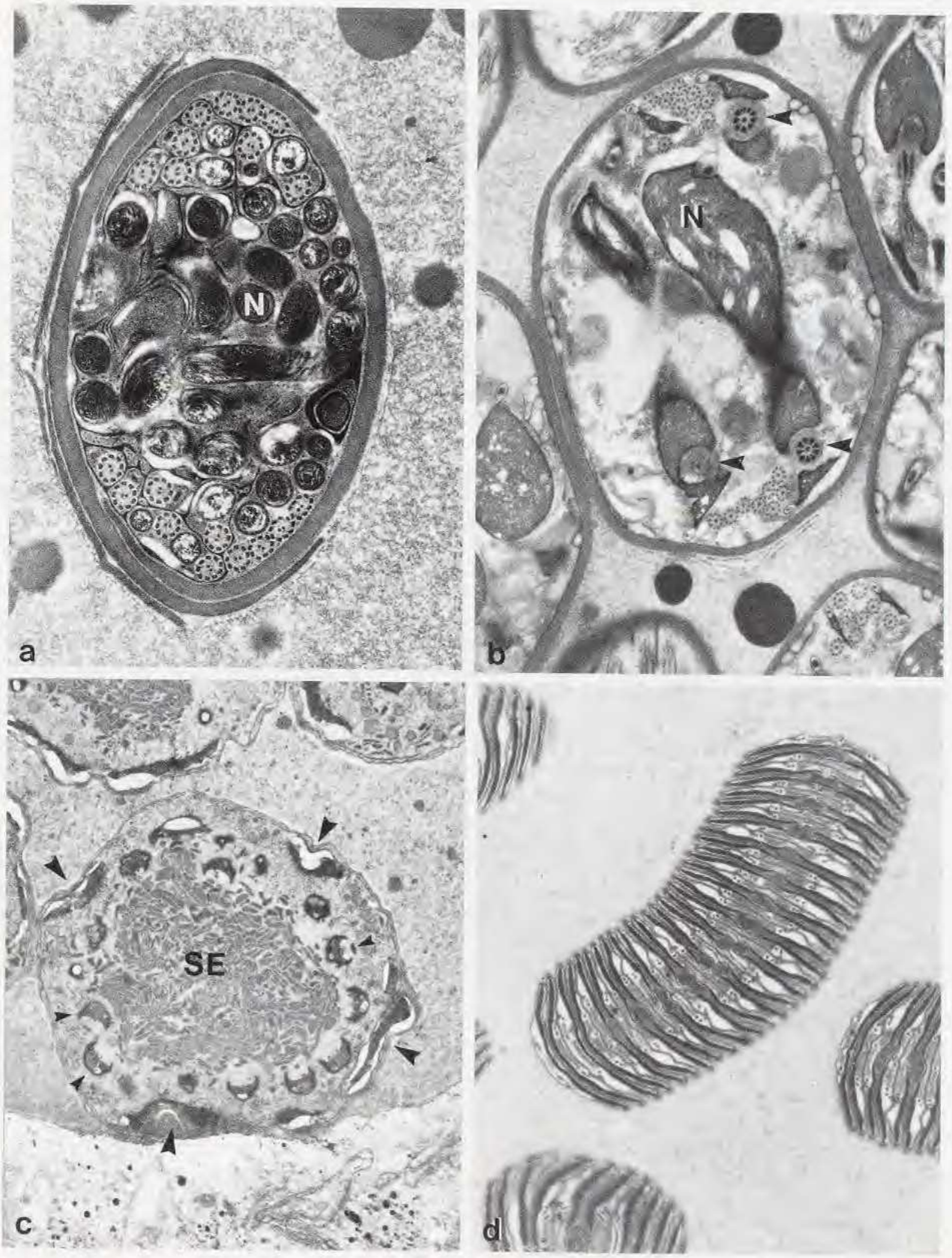
In actinotrichid mites, e.g. spider mites (Tetranychidae), spherical spermatozoa become irregular and possess filaments in cell processes, probably enabling amoeboid movements [13, 16, 22, 98].

Acrosomal reaction

The acrosomal reaction of *Limulus polyphemus* is a classical subject of study in spermatology and has been described in detail [29, 47, 124]. Upon contact of the sperm cell with the egg, exocytosis of the acrosomal vacuole occurs. The contents of the vacuole ensures attachment to the egg. In about 4 seconds, a 60 µm long process grows out of the anterior end of the cell (so called true discharge). The process contains the acrosomal filament (perforatorium) which is uncoiled and remains covered by a membrane (the posterior membrane of the acrosomal vacuole to which material derived from the nuclear envelope is continuously added). The elongating process rotates, which helps the process to penetrate the extracellular layers of the egg. According to [47, 129] the driving force which creates the elongation of the process is the consequence of an alteration in the twist of the actin filaments within the acrosomal filament (compare Figs 1a, 3a).

No other chelicerate sperm cell has been investigated with regard to its acrosomal reaction. Because of the structural similarity of the acrosomal complexes of many arachnids it can be assumed that the main events are similar to those known from the xiphosuran (Fig. 3). However, the numerous peculiarities indicated above urgently need a detailed investigation.

FIG. 6. — Transport forms of spermatozoa in Arachnida. **a:** *Cryptocellus boneti* (Ricinulei). The coiled sperm cell is encysted. The cyst wall consists of two dense plates which are intracellular products (see Fig. 3c). Additional secretions are added in the vas deferens [20]. x 19 000. **b:** A synspermium of *Segestria senoculata* (Araneae). Arrowheads point to the bases of three (of four) axonemes [24]. x 13 250. **c:** A sperm ball of *Siro duricorius* (Opiliones-Cyphophthalmi) consists of peripherally arranged infertile sperm cells (large arrowheads) and smaller, cup-like fertile spermatozoa (small arrowheads). In the centre of the ball conspicuous secretions are seen (compare Fig. 2 and [80]). x 3 350. **d:** Pile of 32 spermatozoa arranged in 16 pairs in *Eusimonia mirabilis* (Solifugae) [7]. x 7 500. N, nucleus; SE, secretion.



Phylogenetic and systematic considerations

Sperm cells of Chelicerata are evidently very diverse and the taxon-specificity of these cells offers the possibility to use characteristics of these cells for taxonomic purposes [5, 6, 9, 12, 13, 32, 33, 35, 138].

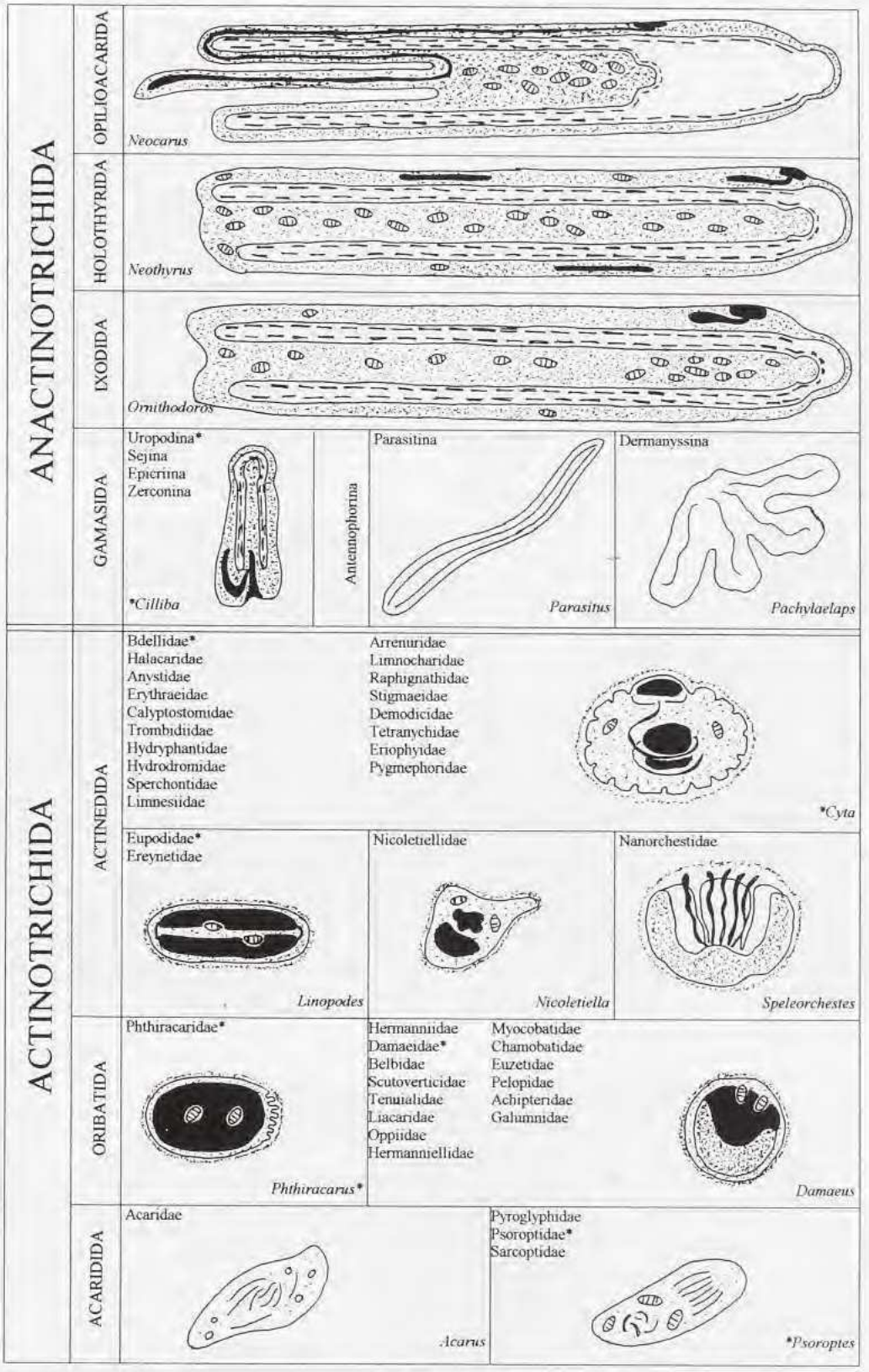
Among the xiphosurans interesting features have been shown already when comparing the only Atlantic species (*Limulus polyphemus*) with the three Indowest-Pacific taxa (*Tachypleus gigas*, *T. tridentatus*, *Carcinoscorpius rotundicauda*). Apart from some deviations in the shape of the acrosomal vesicle, arrangement of mitochondria and acrosomal filament, the most obvious difference is the lack of the central microtubules in the axoneme of the Indowest-Pacific species. This is a synapomorphy of these taxa and demonstrates the result of a long independent evolution [18, 147].

The few studies on Pantopoda have shown considerable differences between the two genera investigated (see above) which corroborates the view that Pycnogonidae is the more derived taxon compared with Nymphonidae [84, 97]. The axonemal pattern may be used to ascertain the validity of certain species (e.g. *Nymphon gracile* and *N. rubrum*) as separate taxa [52].

Within the Arachnida, only in the Opiliones [78, 81, 125] and Acari [5, 6, 9, 13] have systematic considerations been undertaken on the basis of a sufficiently wide range of taxa. Some encouraging aspects emerged also from the recent studies of "Pedipalpi" and Araneae [14, 21, 24, 26, 76, 82, 92, 126].

All of these sperm cells are, despite their wide range of complexity, capable of transferring the male's genetic information to the female germ cell. It is very challenging trying to trace the evolution of the sperm cell through the branching phylogenetic tree looking for a more comprehensive understanding of the alterations of this cell type. It is obvious that this is a long lasting project which leaves much work for the future. Arachnida represent a very old taxon, so there are not only the usual gaps in knowledge (which could be closed by future research) but also those caused by extinction of large taxa [36, 70, 86, 105, 136, 137]. Thus the extant major taxa of Arachnida are quite isolated from each other. Spermatology may provide a tool to bridge gaps in taxonomic understanding between these extant taxa. Furthermore it has to be kept in mind that convergences may also occur at the cellular level. Some examples were already mentioned: displacement of axonemal base to the anterior (*Cryptocellus*/Ricinulei, *Tetragnatha*/Araneae), 9x2 +0 axoneme (*Tachypleus*, *Carcinoscorpius*/Xiphosura, Scorpiones in part, Linyphiidae/Araneae), deep implantation fossa (*Schizomus*/ Uropygi, some Araneae such as *Pholcus*), helical or corkscrew appearance of sperm head (*Buthus*/Scorpiones, Pseudoscorpiones, "Pedipalpi"- Araneae). (In Araneae, this corkscrew appearance in *Pholcus phalangioides* is profoundly different from all other spiders and is thus probably an autapomorphic peculiarity of this taxon) [12, 24] (Fig. 4). Most likely another convergence is demonstrated by the shaping of the spermatid under the influence of "acrosomal" material (*Nemastoma*/Opiliones, vacuolate type of sperm/Acari-Anactinotrichida) (Fig. 8e). Different types of "envelopes" are found in the coiled sperm: extracellular ones (Pseudoscorpiones, "Pedipalpi", Araneae) and intracellular ones (*Cryptocellus*/Ricinulei) (Figs 3e, 6a,b). Some of these convergences are easily recognized by fine structural analysis or observation of spermiogenesis, others need comparison with related taxa on a wider scale.

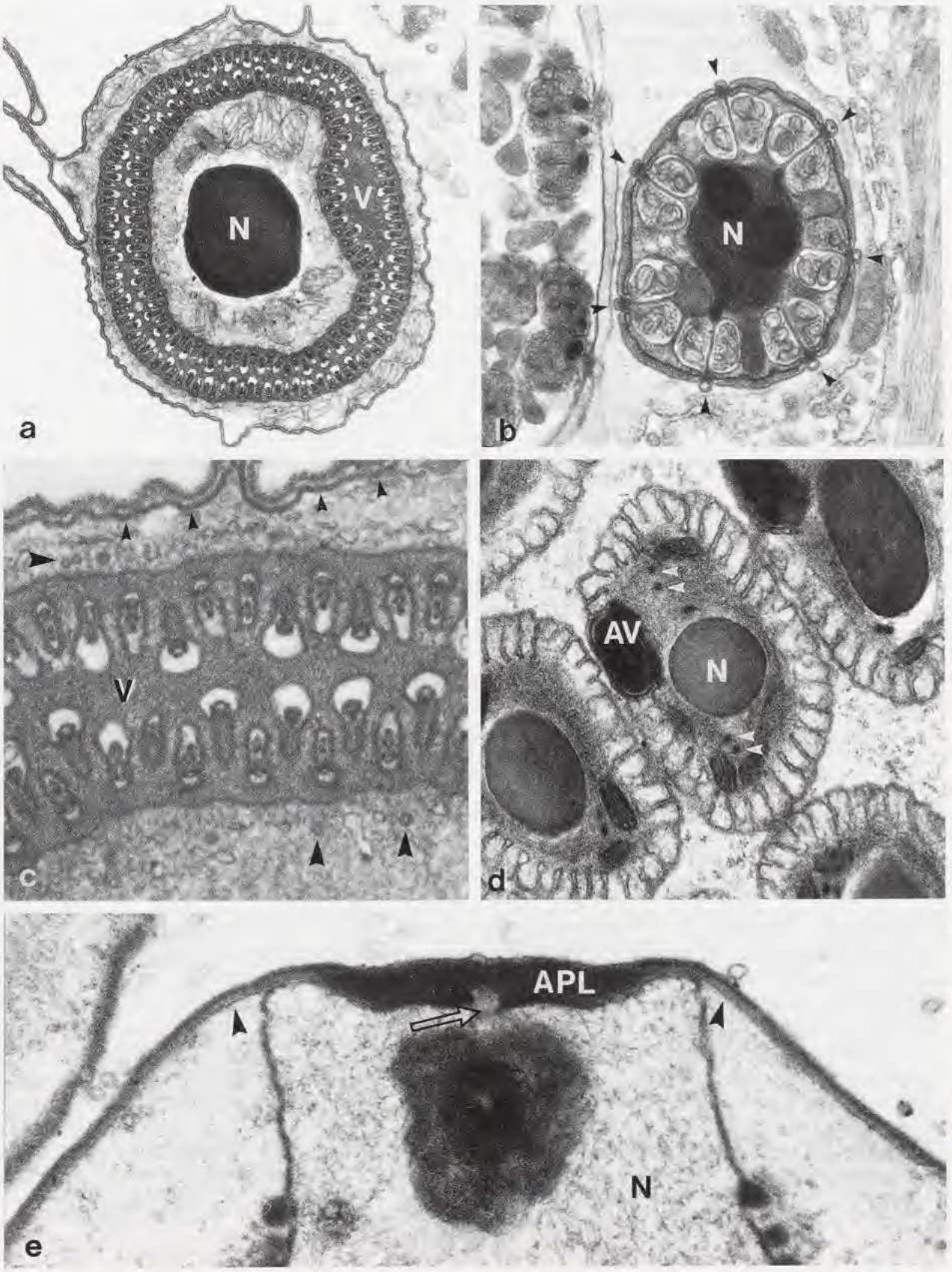
FIG. 7. — Sperm types in Acari. Asterisks indicate genera and corresponding higher taxa [modified from 13]. Spermatozoa of Antennophorina are probably intermediate between vacuolated type and ribbon type [ALBERTI & BLASZAK unpublished]. Note that spermatozoa of Actinedida exhibit a diversity which can hardly be depicted here (compare [6, 13]). See also Fig. 9 with respect to Gamasida.



Thus spermatology may at least shed some new light on systematical interpretations and may induce a reconsideration of certain traditional ideas. Some examples of relationships which were suggested previously and which could be viewed at in the light of the new spermatological findings are: Pseudoscorpiones-Scorpiones [148]; Pseudoscorpiones-Solifugae [69, 114, 117, 136, 137]; Uropygi-Acari [111]; Solifugae-Acari/Actinotrichida [67, 149]; Acari/Anactinotrichida -Acari/Actinotrichida [83, 53, 91, 117, 136, 137]; Opiliones/ Ricinulei-Acari [30, 88]; Opiliones-Acari [83, 108, 114]; Ricinulei-Acari [53, 91, 117]; Ricinulei-Acari/Anactinotrichida [69]; Pedipalpi-Palpigradi [83, 110]; Schizomida-Palpigradi [38, 132]; Palpigradi-Acari/ Actinotrichida [69]. In some cases it was already possible to bridge some gaps or solve open questions.

The well known example of the 9x2+3 axoneme uniting "Pedipalpi" with Araneae was already mentioned (Fig. 3e). This finding was not surprising from the viewpoint of the systematists (who had known for a long time that these taxa are closely related because of other character states: Megoperculata) [137], but it was important to recognize that spermatology may function as a taxonomic tool in Arachnida [21, 76, 103, 107, 112]. However, the main problem with these taxa is concerned with the relationships within the group Megoperculata. Are Uropygi and Amblypygi sister groups and are they together (as Pedipalpi) the sister group of the taxon Araneae [117]? Are Amblypygi and Araneae sister groups (= Labellata) [137] forming the sister group to Uropygi? Does the term "Pedipalpi" thus describe a monophyletic or paraphyletic taxon [71]? Moreover, do the Uropygi really constitute a natural (monophyletic) group? Several authors have divided this taxon into Thelyphonida (=Uropygi *s. strict.*) and Schizomida (= micro whip scorpions) [90, 96, 97]? Are the Palpigradi closely related to the "Pedipalpi" (especially to Uropygi-Schizomida) as several authors have suggested [38, 83, 110, 132; see also 117]? Spermatology may at least point the direction of a solution of these questions (Fig. 5). In Araneae the nucleus of the sperm cell extends with a postcentriolar nuclear elongation beyond the base of the axoneme making the nucleus and the whole cell asymmetrical. In Amblypygi the same asymmetry of the nucleus is found, though less pronounced. Araneae and Amblypygi are thus united by the presence of this nuclear elongation as a synapomorphy (shared derived character). The presence of a middle piece in the Amblypygi and the early derived spider *Heptathela kimurai* (Mesothelae) is, in contrast, considered a symplesiomorphy. On the other hand Thelyphonida and Schizomida do not possess a middle piece and a shortened central triplet in the axoneme. Both characteristics are probable synapomorphies. The helical nucleus is not developed in a corkscrew (with sharpened edges) as in the Amblypygi and Araneae and does not demonstrate a postcentriolar nuclear elongation (symmetrical nucleus). These characteristics are most likely symplesiomorphies of the Uropygi. Thus the spermatological results would support the view that the taxon "Pedipalpi" describes indeed a paraphyletic group. There are no spermatological indications which would support a close relationship with Palpigradi. Schizomida possess the

FIG. 8. — Some characteristics of acarine sperm cells. **a:** Vacuolated-type sperm in *Sejus togatus* (Gamasida-Sejina) in transverse section. Note the wall of the vacuole provided with numerous so called cellular processes (compare c) [11]. x 14 600. **b:** Ribbon-type sperm of *Parasitus berlesei* (Gamasida-Parasitina) sectioned transversely. Note ribbons (arrowheads) with the paired sacs underneath [5]. x 16 500. **c:** Cellular processes in the spermatozoon of *Sejus togatus* (Gamasida-Sejina). Note different profiles according to level of section through the individual processes and filaments within the processes. Large arrowheads indicate microtubules, small arrowheads indicate flat acrosomal cisterna (compare e). x 84 000. **d:** Spermatozoon of *Cyta latirostris* (Actinedida). This type of sperm may be regarded as representative (plesiomorphic) of at least a great part of the very diverse Actinedida (see Fig. 7). Arrowheads indicate coils of the acrosomal filament [6]. x 18 500. **e:** Part of early spermatid of *Epicrius mollis* (Gamasida-Epicriina), which will develop into a vacuolated-type sperm. The acrosomal vacuole has differentiated into an acrosomal plate, to which the nucleus is attached and from which the acrosomal filament arises (arrow), and an extensive flat portion (cisterna) which grows out under the plasmalemma (arrowheads; compare c) [5]. x 27 000. APL, acrosomal plate; AV, acrosomal vacuole; N, nucleus; V, vacuole.



typical 9x2+3 axoneme of "Pedipalpi"-Araneae (synapomorphy of the Megoperculata), Palpigradi have aflagellate spermatozoa (Figs 2, 5). Further it appears that it is not necessary to separate Schizomida from the remaining Uropygi because of the mentioned synapomorphies, despite differences which include the paracrosomal lattice structure appearing in the late spermatid of *Schizomus* as a transient structure (Figs 3d, 5). The position of the acrosomal filament and the deep implantation fossa are most remarkable (Fig. 5) [21, 24, 76, 107, 126].

Within the Araneae it was shown that spermatozoa can be transferred to the female as numerous individual cells, each surrounded by its own sheath (cleistospermia), as numerous aggregates of individual cells, surrounded by a common sheath (coenospermia), as one tubular "spermatophore" (only in Telemidae) or as numerous syncytial spermatozoa (synspermia) (see above).

Though only few taxa have been studied with respect to these transport-forms it appears that the coenospermia are plesiomorphic since these have been observed in the early derived liphistiomorph spiders [HAUPT & KOVOOR, 1988 pers. comm.; ALBERTI, HAUPT & SCHWENDINGER, unpublished]. Furthermore, representatives of several families of orthognath spiders (Atypidae, Antrodiaetidae, Nemesiidae, Dipluridae, Theraphosidae) and of the labidognath spider family Filistatidae [24, 26, ALBERTI & COYLE unpublished, ALBERTI, HAUPT & SCHWENDINGER, unpublished] possess this type of encapsulated sperm. The "spermatophore" of Telemidae is regarded by the present author as an autapomorphy of this group of cave dwelling spiders since it has been observed only in this family (thus representing a rather isolated phenomenon within spiders) and does not show any relationship with spermatophores of Amblypygi, the assumed sister group of spiders. It is formed not by accessory glands, which are usually involved in spermatophore construction, but by secretions of the vasa deferentia [82]. Thus these "spermatophores" are established in the same region of the genital tract as the coenospermia and are most likely a special modification of these [12, 15, 24].

Synspermia are obviously an apomorphy. This type of sperm aggregation is not found elsewhere within the Arachnida and probably the animal kingdom. Until now, it has been observed only in the families Segestriidae, Dysderidae, Scytodidae and Sicariidae. It therefore may represent a synapomorphy uniting these (and other?) families of so-called haplogyne spiders, a group of Araneae which offers many systematical problems [46, 115] (Figs 3e, 6b).

The functional significance of the astonishingly diverse spermatozoa of Araneae, regarding the general uniform mode of insemination with the male palpal organ, has yet to be fully understood (see also Conclusions). However, the knowledge of spermatology is developed further in this functional respect and also with regard to systematical interpretations in Acari [5, 6, 9, 11, 13, 17].

The Acari are most often considered to be related to the Opiliones and/or Ricinulei [see 69, 70, 91, 117, 136, 137 for detailed discussions]. Other candidates are Solifugae and Palpigradi [67, 69, 70, 149]. However, it has long been debated what comprise the Acari. Are the Acari polyphyletic, diphyletic or monophyletic [see 129]? Aside of some extreme views which for example regarded the Opilioacarida or the Ixodida as independent arachnid groups or at least far separate from the (other) Acari [see 111, 116, 123], in the last decades two suggestions have mainly been discussed. Some authors support the idea that there are three (Opilioacarida, Anactinotrichida, Actinotrichida) major acarine groups [68, 79, 83] others think of two (Anactinotrichida including Opilioacarida, Actinotrichida) [53, 55, 69, 70, 85, 91, 97, 150]. Spermatology has contributed to these questions the following: from the sperm morphology of Opilioacarida, which is almost identical with that of Ixodida (ticks) and certain Gamasida, it is obvious that these taxa constitute one group: Anactinotrichida (=Parasitiformes). The vacuolated type of sperm is a synapomorphy of this group (Fig. 7). On the other hand it was demonstrated that the spermatozoa of Actinotrichida (=Acariformes) do not have anything in common with

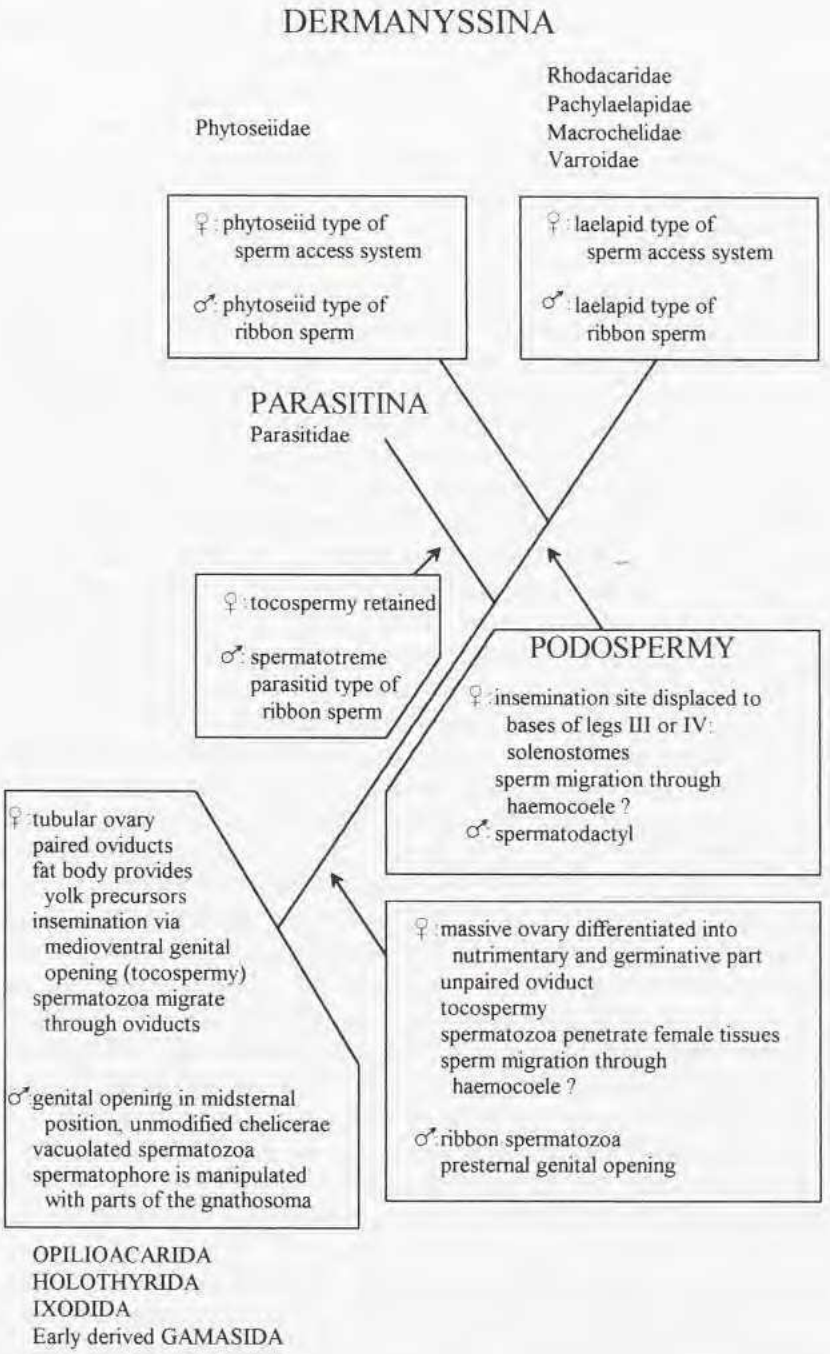


FIG. 9. — Diagram depicting probable evolutionary changes of genital systems and sperm morphology in Gamasida [13]. Only those gamasid families from which fine structural results are available are listed. Tocospermy: insemination via the primary genital opening; podospermy: insemination via secondary copulation pores (= solenostomes). Spermatotreme: slit in the mobile digit of the chelicera to hold the neck of the spermatophore during its transfer; spermatodactyl: slender process at the mobile digit of the chelicera used to transfer the sperm.

those of Anactinotrichida what could be termed a synapomorphy [5, 6, 9, 13]. Thus, it is at least a misleading simplification to consider the sperm cells of, for instance, Ixodida, as typical for the Acari as a whole (Fig. 7).

The problem of systematics of major groups of Acari is reduced by spermatological data to diphyly versus monophyly, with two different sperm types to be compared with each other and with those of the candidates outside the Acari (e.g. Ricinulei and Opiliones-Anactinotrichida; Solifugae and Palpigradi-Actinotrichida). No decision solving these questions for sister group relationships can yet be made (compare Fig. 2). The evolutionary distance between these taxa is probably too large [see for details 13]. At present the spermatological data also do not indicate that one of the major mite groups developed from part of the other, which would then be a paraphyletic taxon [see 30, 88].

Comparing sperm cells of Acari on a broad basis of taxa it was possible first to detect the profound difference between spermatozoa of Anactinotrichida and Actinotrichida (Fig. 7). Further, within the Anactinotrichida the vacuolated type turned out to be the plesiomorphic type from which other types (ribbon type and its subtypes) have developed [5, 6, 9, 13, 17, 139-141]. From this basis it was, at least in part, possible to trace the evolution of the sperm cell within the Anactinotrichida (Fig. 9). It was deduced that the vacuolated and ribbon type are correlated with different modes of insemination. In those taxa possessing vacuolated spermatozoa (Ixodida, Gamasida in part) sac like spermatophores are transferred to the female (reproductive behaviour of Opilioacarida and Holothyrida is not known). The gnathosoma manipulates the very complex spermatophore [53, 61] to the female genital opening located medioventrally. Capacitated spermatozoa (see above) migrate through the oviducts into the tubular ovary where fertilization of oocytes, most likely, occurs [43]. In those taxa having the ribbon type (Gamasida in part: Parasitina and Dermanyssina), the ovary comprises a nutritive tissue probably derived from sister cells of the oocytes [3, 25]. The ovary is a solid organ. It is thus necessary that female tissues are penetrated by the ribbon spermatozoa during their migration to the oocytes. There is growing evidence that this penetration results in a migration of spermatozoa through the haemocoele in Parasitina to the ovary [11, 13]. In Dermanyssina specialized paired sperm induction pores are found in a peculiar lateral position at the bases of legs III or IV [11, 17, 31, 50, 54, 57]. The question is, how was it possible to change the fertilization site during evolution of these taxa with spermatozoa apparently extremely derived (vacuolated type) and adapted to special conditions of the female genital system. However, knowing the situation in Parasitina it is not so difficult to understand this dislocation of the site of sperm transfer. Only the penetration site had to be displaced. Spermatophores were already manipulated with the chelicerae (Parasitina and Dermanyssina males have transformed chelicerae for this purpose: spermatotrema, spermatodactyl) and spermatozoa, of the ribbon type, were already adapted to penetration and migration through female tissues. Further adaptations are found in Dermanyssina regarding a new sperm access system which leads the sperm cells from the induction pores (solenostomes) to the ovary, displacement of the male genital opening into a presternal position and reorganization of the female genital tract and these in turn result in alterations of spermatozoa of the ribbon type to a less complex structure compared to the vacuolated type or the ribbon type of the Parasitina [11, 13, 17].

These interpretations which are based primarily on spermatological results, combined with studies on anatomy, histology and oogenesis, may very well play a key role in understanding the large group of Anactinotrichida and its most successful (species-rich) taxa Parasitina and Dermanyssina (Fig. 9). Evidently the modifications can be interpreted in the sense of economy, with the development of a nutritive tissue (so called lyrate organ) [95] in Parasitina and Dermanyssina as the initial event [11, 13, 17, 25]. It is of interest that comparable differentiations occurred in the Acari/Actinotrichida within the spider mites (Tetranychidae: direct sperm transfer with penis, migration of spermatozoa through haemocoele, nutritive cells in the ovary) and

Acaridida (penis, secondary copulatory pore, sperm access system leading to ovary) by convergence [13, 16, 22, 98, 145].

Thus the case of the Acari not only demonstrates the usefulness of comparative spermatology in solving systematical problems. It also gives an impression how sperm diversity has been evolved parallel to phylogenetic alterations with their functional/adaptive implications in a restricted taxon.

Conclusion and perspective

Though in recent years knowledge on sperm structure in Chelicerata has increased considerably, many questions remain unsolved. Indeed, the growth in knowledge has shown that yet more fascinating problems remain to be investigated only some of which can be indicated here.

First, spermatozoa of several taxonomic groups are only known from one (Solifugae, Ricinulei, Palpigradi) or very few species (e.g. Uropygi, Amblypygi) and it is evidently necessary to examine further representatives. From Solifugae only mature spermatozoa are known and studies on spermatogenesis are urgently required to understand the very peculiar sperm morphology as well as the aggregations which they form (Fig. 6d).

Capacitation processes are only known in (structural) detail from tick spermatozoa and similar events (e.g. the turning inside out-process, only to mention the most striking event) probably occur also in the vacuolated sperm of the other taxa. But there are indications of capacitation of sperm of other acarine taxa (e.g. Anactinotrichida: *Varroa jacobsoni*; Actinotrichida: *Tetranychus urticae, Bdella septentrionalis, Phytoptus avellanae, Acarus siro and Tyrophagus putrescentiae*) [5, 17, 19, 22, 23, 144].

In spiders, the synspermia of Dysderidae and also the cleistospermia of Oonopidae possess large vacuoles [see above, 24]. Probably these facilitate the process of uncoiling in the female. The organelles such as acrosomal vacuole, nucleus and axoneme, are covered with membranes of the vesicles/vacuole, which could be integrated into the plasmalemma very quickly. Thus these spermatozoa may be regarded as "precapacitated" (being somewhat similar by convergence to the vacuolate sperm cells of the mentioned Acari-Anactinotrichida) (see also vesicles at the periphery of sperm of Uropygi and Amblypygi; Fig. 2). As the female genital tract of spiders differs considerably [65], these and other specializations (e.g. the lack of mitochondria in some spiders) may represent adaptations to these various fertilization conditions. These problems evidently offer a broad field for exciting future studies which may be considered under the aspects of sperm competition and securing sperm priority.

Except for *Limulus polyphemus* sperm, nothing is known about acrosomal reactions in chelicerate sperm cells [124]. In most taxa the exact site where the eggs are fertilized is unknown or at least speculative. Evidently sperm cells pass through the haemolymphatic space in certain mites (Acari: Parasitidae, Tetranychidae). Are these exceptions or do further examples exist? Apparently this passage brought about the development of new genital ducts (sperm access system in Dermanyssina) as a reaction of the female comparable to the paragenitalia in bed bugs and their relatives. This in turn indicates the strong selective influence which is imposed by the females not only on the male genitalia but also on spermatozoa [see e.g. 11, 13, 17, 51].

Only few chelicerate sperm cells have been investigated with regard to their cytochemistry: *Limulus polyphemus* [124] and two gamasid mites [143]. The significance of the many enigmatic components (vacuoles, vesicles, dense streaks, plates, various filaments, inclusion bodies, etc.) could be better understood using appropriate and available methods.

Even in those groups in which a broad range of taxa has been investigated, such as Araneae and Acari, much work is still to be done. Araneae offer many questions, for instance: what is the functional significance of the various transport-forms (coenospermia, cleistospermia, synspermia, "spermatophores")? Is this diversity related to the male and female copulatory organs which are

insufficiently understood [see 65, 73, 87, 121, 122, 128]. How are these encapsulated spermatozoa activated and how do they then function? What happens to the enigmatic synspermia in the female?

Sperm aggregates of Solifugae and the enigmatic small opilionids of the genus *Siro* need further investigation. The latter taxon is the only one within the Chelicerata known to have dimorphic spermatozoa, albeit of unknown functional significance. Does this phenomenon also occur in other Cyphophthalmi?

The peculiar genital tract of "Pedipalpi", possessing a pair of glands with holocrine secretion of a very unconventional type, offers very exciting interpretations. If these glands could be proven to be of testicular origin, the secretory products could represent strongly modified germ cells too. This interpretation would be of much interest regarding the relationships between "Pedipalpi" and Araneae [see above and 13].

The adaptations of sperm cells being transferred via various types of secreted containers (capsules, stalked spermatophores of various complexity) [see e.g. with regard to Acari: 27, 61, 64, 146] need to be studied in more detail.

Only few studies have focused on the association of microorganisms with spermatozoa [2, 59, 62]. In particular the enigmatic *Adlerocystis* sp. which is a regular symbiotic associate of tick spermatozoa deserves more attention [62].

In Acari a broad range of sperm cells from a very high complexity to very "simple" cells is observable (Figs 7, 8) All these cells transfer genetic material apparently successfully. Many taxa, however, reproduce exclusively parthenogenetically [100]. This is in particular remarkable regarding the oribatid mites, a very common group living in almost all soils. It has been suggested that in certain taxa a reversion to sexuality may have occurred [99]. An even more striking example is represented by the Acaridida (flour mites, house dust mites, feather mites, itch and mange mites etc.), which reproduce bisexually and have probably developed from within a certain group of oribatids which is known to reproduce exclusively by parthenogenesis. The idea has been suggested (as the most parsimonious one) that the Acaridida developed bisexuality, and thus sperm cells, secondarily [99, 100].

Mites demonstrating the most diverse reproductive behaviour are probably one of the most promising groups to study the complex interrelationships between behavioural, morphological and cytological evolutionary processes on a comparative basis in Chelicerata. Such a study almost certainly would give further material for improving systematical concepts.

ACKNOWLEDGEMENTS

The author wishes to express his thanks to the numerous persons who assisted in many respects to make this study possible. Among all these three played a major role: the late Prof. Dr. A. REMANE (Kiel) as the impressive teacher of animal morphology, Prof. Dr. R. SCHUSTER (Graz, previously Kiel), who introduced the author to the exciting sciences of Acarology and Arachnology, and Prof. Dr. V. STORCH (Heidelberg, previously Kiel), who opened the door into the fascinating world of comparative ultrastructure research.

REFERENCES

1. AFZELIUS, B. A., 1979. — Sperm structure in relation to phylogeny in lower metazoa. *In:* D. W. FAWCETT & J. M. BEDFORD, *The Spermatozoon*. Baltimore & München, Urban & Schwarzenberg: 243-251.

2. AFZELIUS, B. A., ALBERTI, G., DALLAI, R. GODULA, J. & WITALINSKI, W., 1991. — Virus- and Rickettsia-infected sperm cells in arthropods. *Journal of Invertebrate Pathology*, **53**: 365-377.

3. AKIMOV, I. A. & YASTREBTSOV, A. V., 1984. — Reproductive system of *Varroa jacobsoni*. 1. Female reproductive system and oogenesis. *Vestnik Zoologii*, **1984** (6): 61-68.

4. ALBERTI, G., 1979. — Zur Feinstruktur der Spermien und Spermiocytogenese von *Prokoenenia wheeleri* (Rucker, 1901) Palpigradi, Arachnida). *Zoomorphologie*, **94**: 111-120.

5. ALBERTI, G., 1980a. — Zur Feinstruktur der Spermien und Spermiocytogenese der Milben (Acari). I. Anactinotrichida. *Zoologische Jahrbücher. Abteilung für Anatomie*, **104**: 77-138.

6. ALBERTI, G., 1980b. — Zur Feinstruktur der Spermien und Spermiocytogenese der Milben (Acari). II. Actinotrichida. *Zoologische Jahrbücher. Abteilung für Anatomie*, **104**: 144-203.

7. ALBERTI, G., 1980c. — Zur Feinstruktur des Hodenepithels und der Spermien von *Eusimonia mirabilis* Roewer, 1934 (Solifugae, Arachnida). *Zoologischer Anzeiger*, **204**: 345-252.

8. ALBERTI, G., 1983. — Fine structure of scorpion spermatozoa (*Buthus occitanus*; Buthidae, Scorpiones). *Journal of Morphology*, **177**: 205-212.

9. ALBERTI, G., 1984. — The contribution of comparative spermatology to problems of acarine systematics. *In:* D. A. GRIFFITHS & C. E. BOWMAN, *Acarology VI*. Chichester, Ellis Horwood. **I**: 479-490.

10. ALBERTI, G., 1988a. — Sperm aggregations in arachnids. *In:* J. HAUPT, *XI. Europäisches Arachnologisches Colloquium*. Berlin, Technische Universität Berlin, **38**: 331.

11. ALBERTI, G., 1988b. — Genital system of Gamasida and its bearing on phylogeny. *In:* G. P. CHANNA BASAVANNA & C. A. VIRAKTAMATH, *Progress in Acarology*. New Delhi, Oxford & IBH Publishing. **I**: 197-204.

12. ALBERTI, G., 1990. — Comparative spermatology of Araneae. *Acta Zoologica Fennica*, **190**: 17-34.

13. ALBERTI, G., 1991a. — Spermatology in the Acari: systematic and functional implications. *In:* R. SCHUSTER & P. W. MURPHY, *The Acari - Reproduction, Development and Life-History Strategies*. London, Chapman & Hall: 77-105.

14. ALBERTI, G., 1991b. — On sperm ultrastructure and systematics of Arachnida with special emphasis on Araneae and Acari. *In:* B. BACCETTI, *Comparative Spermatology 20 Years After*. New York, Raven Press: 929-936.

15. ALBERTI, G. & COYLE, F. A., 1991. — Ultrastructure of the primary male genital system, spermatozoa, and spermiogenesis of *Hypochilus pococki* (Araneae, Hypochilidae). *Journal of Arachnology*, **19**: 136-149.

16. ALBERTI, G. & CROOKER, A. E., 1985. — Internal anatomy. *In:* W. HELLE, *World Crop Pests, Vol. IA. Spider Mites and their Control*. Amsterdam, Elsevier: 29-62.

17. ALBERTI, G. & HÄNEL, H., 1986. — Fine structure of the genital system in the bee parasite, *Varroa jacobsoni* (Gamasida: Dermanyssina) with remarks on spermiogenesis, spermatozoa, and capacitation. *Experimental & Applied Acarology*, **2**: 63-104.

18. ALBERTI, G. & JANSSEN, H.-H., 1986. — On the fine structure of spermatozoa of *Tachypleus gigas* (Xiphosura, Merostomata). *International Journal of Invertebrate Reproduction and Development*, **9**: 309-319.

19. ALBERTI, G. & NUZZACI, G. in press. — Oogenesis and spermatogenesis. *In:* W. HELLE, *World Crop Pests. Vol. 6. Eriophyoid Mites: Their Biology, Natural Enemies and Control*. Amsterdam, Elsevier.

20. ALBERTI, G. & PALACIOS-VARGAS, J. G., 1984. — Fine structure of spermatogenesis and mature spermatozoa of *Cryptocellus boneti* Bolivar y Pieltain, 1941 (Arachnida, Ricinulei). *Journal of Ultrastructure Research*, **87**: 1-12.

21. ALBERTI, G. & PALACIOS-VARGAS, J. G., 1987. — Fine structure of spermatozoa and spermatogenesis of *Schizomus palaciosi*, Reddell and Cokendolpher, 1986 (Arachnida: Uropygi, Schizomida). *Protoplasma*, **137**: 1-14.

22. ALBERTI, G. & STORCH, V., 1976a. — Ultrastruktur-Untersuchungen am männlichen Genitaltrakt und an Spermien von *Tetranychus urticae* (Tetranychidae, Trombidiformes). *Zoomorphologie*, **83**: 183- 296.

23. ALBERTI, G. & STORCH, V., 1976b. — Spermiocytogenese, Spermien und Spermatophore von Schnabelmilben (Bdellidae, Acari). *Acta Zoologica (Stockholm)*, **57**: 177-188.

24. ALBERTI, G. & WEINMANN, C., 1985. — Fine structure of spermatozoa of some labidognath spiders (Filistatidae, Segestriidae, Dysderidae, Oonopidae, Scytodidae, Pholcidae; Araneae; Arachnida) with remarks on spermiogenesis. *Journal of Morphology*, **185**: 1-35.

25. ALBERTI, G. & ZECK.KAPP, G., 1986. — The nutrimentary egg development of the mite, *Varroa jacobsoni* (Acari, Arachnida), an ectoparasite of honey bees. *Acta Zoologica (Stockholm)*, **67**: 11-25.

26. ALBERTI, G., AFZELIUS, B. A. & LUCAS, S. M., 1986. — Ultrastructure of spermatozoa and spermatogenesis in bird spiders (Theraphosidae, Mygalomorphae, Araneae). *Journal of Submicroscopic Cytology*, **18**: 739-753.

27. ALBERTI, G., FERNANDEZ, N. A. & KÜMMEL, G., 1991. — Spermatophores and spermatozoa of oribatid mites (Acari: Oribatida). Part II: Functional and systematical considerations. *Acarologia*, **32**: 435-449.

28. ANDRÉ, J., 1959. — Étude au microscope électronique de l'évolution du chondriome pendant la spermatogenèse du scorpion *Euscorpius flavicaudis*. *Journal of Ultrastructure Research*, **2**: 288-308.

29. ANDRÉ, J., 1965. — À propos d'une leçon sur la limule. *Annales de la Faculté des Sciences de l'Université de Clermont*, **26**: 27-37.

30. ANDRÉ, M. & LAMY, E., 1937. — *Les idées actuelles sur la phylogénie des Acariens*. Paris, chez l'auteur: 1-148.

31. ATHIAS-HENRIOT, C., 1968. — L'appareil d'insémination laelapoïde (Acariens anactinotriches: Laelapoidea). Premières observations. Possibilité d'emploi à fins taxonomiques. *Bulletin Scientifique de Bourgogne*, **25**: 175-228.

32. BACCETTI, B., 1979. — Ultrastructure of sperm and its bearing on arthropod phylogeny. *In:* A. P. GUPTA, *Arthropod Phylogeny*. New York, Van Nostrand Reinhold: 609-644.

33. BACCETTI, B., 1985. — Evolution of the sperm cell. *In:* C. B. METZ & A. MONROY, *Biology of Fertilization. Vol. 2. Biology of The Sperm*. Orlando, Academic Press: 3-58.

34. BACCETTI, B., 1987. — News on phylogenetical and taxonomical spermatology. *In:* H. MOHRI, *New Horizons in Sperm Cell Research*. Tokyo, Japan Scientific Societies Press: 333-348.

35. BACCETTI, B. & AFZELIUS, B. A., 1976. — *The Biology of the Sperm Cell*. Monographs in Developmental Biology. Vol. 10. Munich, S. Karger: 1-254.

36. BERGSTRÖM, J., 1979. — Morphology of fossil arthropods as a guide to phylogenetic relationships. A. P. GUPTA, *Arthropod Phylogeny*. New York, Van Nostrand Reinhold: 3-56.

37. BERTKAU, P., 1877. — Über die Übertragungsorgane und die Spermatozoen der Spinnen. *Verhandlungen des Naturhistorischen Vereins preussischer Rheinlande*, **34**: 28-32.

38. BÖRNER, C., 1904. — *Beiträge zur Morphologie der Arthropoden. I. Ein Beitrag zur Kenntnis der Pedipalpen*. Stuttgart, E. Nägele: 1-174, pl. I-VII.

39. BOISSIN, L., 1973. — Étude ultrastructurale de la spermiogenèse de *Meta bourneti* Simon (Arachnides, Araneides, Metinae). *Comptes Rendus de la 2e Réunion d'Arachnologie d'Expression Française, Montpellier*: 7-22.

40. BOISSIN, L., 1974. — Étude ultrastructurale de la spermiogenèse de *Garypus beauvoisi* (Sav.) (Arachnides, Pseudoscorpions). *Archives de Zoologie Expérimentale et Générale*, **115**: 169-184.

41. BREUCKER, H. & HORSTMANN, E., 1968. — Die Spermatozoen der Zecke *Ornithodorus moubata* (Murr.). *Zeitschrift für Zellforschung und mikroskopische Anatomie*, **88**: 1-22.

42. BREUCKER, H. & HORSTMANN, E., 1972. — Die Spermatogenese der Zecke *Ornithodorus moubata* (Murr.). *Zeitschrift für Zellforschung und mikroskopische Anatomie*, **123**: 18-46.

43. BRINTON, L. P., BURGDORFER, W. & OLIVER, J. H. Jr., 1974. — Histology and fine structure of spermatozoa and egg passage in the female tract of *Dermacentor andersoni* Stiles (Acari, Ixodidae). *Tissue and Cell*, **6**: 109-125.

44. BROWN, G. G., 1976. — Scanning electron microscopical and other observations of sperm fertilization reactions in *Limulus polyphemus* L. (Merostomata: Xiphosura). *Journal of Cell Science*, **22**: 547-562.

45. BROWN, S. G., 1985. — Mating behavior of the golden-orb-weaving spider, *Nephila clavipes*: II. Sperm capacitation, sperm competition, and fecundity. *Journal of Comparative Psychology*, **99**: 167-175.

46. CODDINGTON, J. A. & LEVI, H. W., 1991. — Systematics and evolution of spiders. *Annual Review of Ecology and Systematics*, **22**: 565- 592.

47. DE ROSIER, D. J. & TILNEY, L. G., 1991. — The role of actin and actin-binding proteins in the extension of the acrosomal process of *Limulus* sperm. *In:* B. BACCETTI, *Comparative Spermatology 20 Years After*. New York, Raven Press: 149-154.

48. DEURS, B. VAN, 1974a. — Pynogonid sperm. an example of inter- and intraspecific axonemal variation. *Cell and Tissue Research*, **149**: 105-111.

49. DEURS, B. VAN, 1974b. — Spermatology of some Pycnogonida (Arthropoda), with special reference to a microtubule-nuclear envelope complex. *Acta Zoologica (Stockholm)*, **55**: 151-162.

50. DOSSE, G., 1959. — Über den Kopulationsvorgang bei Raubmilben aus der Gattung *Typhlodromus* (Acar., Phytoseiidae). *Pflanzenschutzberichte*, **22**: 125-133.

51. EBERHARD, W. G., 1985. — *Sexual Selection and Animal Genitalia*. Cambridge, Harvard University Press: 1-231.

52. EL-HAWAWI, A. S. N. & KING, P. E., 1978. — Spermiogenesis in a pycnogonid *Nymphon gracile* (Leach). *Journal of Submicroscopic Cytology*, **10**: 345-356.

53. EVANS, G. O., 1992. — *Principles of Acarology*. Wallingford, C. A. B. International: 1-563.

54. EVANS, G. O. & TILL, W. M., 1979. — Mesostigmatic mites of Britain and Ireland (Chelicerata: Acari-Parasitiformes). An introduction to their external morphology and classification. *Transactions of the Zoological Society of London*, **35**: 139-270.

55. EVANS, G. O., SHEALS, J. G. & MACFARLANE, D., 1961. — *The Terrestrial Acari of the Britsh Isles. An introduction to Their Morphology, Biology and Classification*. Vol. 1. London, British Museum (Natural History): 1-219.

56. FAHRENBACH, W. H., 1973. — Spermiogenesis in the horseshoe crab *Limulus polyphemus*. *Journal of Morphology*, **140**: 31-52.

57. FAIN, A., 1963. — La spermathèque et ses canaux adducteurs chez les acariens mésostigmatiques parasites des voies respiratoires. *Acarologia*, **5**: 463-479.

58. FAWCETT, D. W., ANDERSON, W. A., & PHILLIPS, D. M., 1971. — Morphogenetic factors influencing the shape of the sperm head. *Developmental Biology*, **26**: 220-251.

59. FELDMANN-MUHSAM, B., 1974. — Extracellular symbionts of tick sperm. *In:* L. ARVY, *Recherches Biologiques Contemporaines*. Nancy, Vagner: 47-59.

60. FELDMANN-MUHSAM, B., 1986a. — On 5 types of movement of sperm cells of ticks. *Development, Growth & Differentiation*, **28** supplement: 58.

61. FELDMANN-MUHSAM, B., 1986b. — Observations on the mating behaviour of ticks. *In:* J. R. SAUER & J. A. HAIR, *Morphology, Physiology, and Behavioral Biology of Ticks*. Chichester, Ellis Horwood: 217-232.

62. FELDMANN-MUHSAM, B., 1991. — The role of *Adlerocystis* sp. in the reproduction of argasid ticks. *In:* R. SCHUSTER & P. W. MURPHY, *The Acari. Reproduction, Development and Life-history Strategies*. London, Chapman & Hall: 179-190.

63. FELDMANN-MUHSAM, B. & FILSHIE, B. K., 1979. — The ultrastructure of the prospermium of *Ornithodoros* ticks and its relation to sperm maturation and capacitation. *In:* D. W. FAWCETT & J. M. BEDFORD, *The Spermatozoon*. Baltimore & München, Urban & Schwarzenberg: 355-369.

64. FERNANDEZ, N. A., ALBERTI, G. & KÜMMEL, G., 1991. — Spermatophores and spermatozoa of oribatid mites (Acari: Oribatida). Part 1: Fine structure and histochemistry. *Acarologia*, **32**: 261-286.

65. FORSTER, R. R., 1980. — Evolution of the tarsal organ, the respiratory system and the female genitalia in spiders. *8. Internationaler Arachnologen-Kongress Wien*. Verhandlungen. Wien, Egermann: 269-284.

66. FRANZÉN, A., 1956: On spermiogenesis, morphology of the spermatozoon, and biolgy of fertilization among invertebrates. *Zoologiska Bidrag fran Uppsala*, 31: 255-482.

67. GRANDJEAN, F., 1954. — Étude sur les Palaeacaroides (Acariens, Oribates). *Mémoires du Muséum National d'Histoire naturelle, A, série Zoologie*, **7**: 179-274.

68. GRANDJEAN, F., 1969. — Stases. Actinopiline. Rappel de ma classification des acarines en 3 groupes majeurs. Terminologie en soma. *Acarologia*, **11**: 796-827.

69. HAMMEN, L. VAN DER, 1977. — A new classification of Chelicerata. *Zoologische Mededelingen (Leiden)*, **51**: 307-319.

70. HAMMEN, L. VAN DER, 1989. — *An Introduction to Comparative Arachnology*. The Hague, SPB Academic: 1-576.

71. HENNIG, W., 1950. — *Grundzüge einer Theorie der phylogenetischen Systematik*. Berlin, Deutscher Zentralverlag: 1-370.

72. HOOD, R. D., WATSON, O. F., DEASON, T. R. & BENTON, C. L. B., 1972. — Ultrastructure of scorpion spermatozoa with atypical axonemes. *Cytobios*, **5**: 162-177.

73. HUBER, B. A., 1993. — Genital mechanics and sexual selection in the spider *Nesticus cellulanus* (Araneae: Nesticidae). *Canadian Journal of Zoology*, **71**: 2437-2447.

74. JAMIESON, B. G. M., 1986. — Onychophoran — euclitellate relationships: evidence from spermatozoal ultrastructure. *Zoologica Scripta*, **15**: 141-155.

75. JAMIESON, B. G. M., 1987. — *The Ultrastructure and Phylogeny of Insect Spermatozoa*. Cambridge, Cambridge University Press: 1-320.

76. JESPERSEN, A., 1978. — The fine structure of spermiogenesis in the Amblypygi and the Uropygi (Arachnida). *Zoomorphologie*, **89**: 237-250.

77. JESPERSEN, A. & HARTWICK, R., 1973. — Fine structure of spermiogenesis in scorpions from the family Vejovidae. *Journal of Ultrastructure Research*, **45**: 366-383.

78. JONES, ST. R. & COKENDOLPHER, J. C., 1985. — Spermatogenesis in the harvestman *Vonones sayi* (Simon) (Opiliones: Laniatores: Cosmetidae). *Bulletin of the British arachnological Society*, **6**: 403-413.

79. JOHNSTON, D. E., 1982. — Acari. *In:* S. P. PARKER, *Synopsis and Classification of Living Organisms*. New York, Mac Graw Hill. **2**: 111-117.

80. JUBERTHIE, C., MANIER, J.-F. & BOISSIN, L., 1976. — Étude ultrastructurale de la double spermiogenèse chez l'opilion cyphophthalme *Siro rubens* Latreille. *Journal de Microscopie et de Biologie Cellulaire*, **25**: 137-148.

81. JUBERTHIE, C. & MANIER, J.-F., 1978. — Étude ultrastructurale comparée de la spermiogenèse des Opilions et son intérêt phylétique. *In:* P. MERRETT, *Arachnology. Seventh International Congress. Symposia of the Zoological Society of London. Number 42*. London, Academic Press: 407-416.

82. JUBERTHIE, C., LOPEZ, A. & KOVOOR, J., 1981. — Spermiogenesis and spermatophore in *Telema tenella* Simon (Araneae, Telemidae) — An ultrastructural study. *International Journal of Invertebrate Reproduction*, **3**: 181-191.

83. KAESTNER, A., 1965. — *Lehrbuch der Speziellen Zoologie*. Band I. Wirbellose, 1. Teil. 2. Aufl. Suttgart, G. Fischer: 1-845.

84. KING, P. E., 1973. — *Pycnogonids*. London, Hutchinson: 1-144.

85. KRANTZ, G. W., 1978. — *A Manual of Acarology. 2nd ed.* Corvallis, Oregon State University: 1-163.

86. KRAUS, O., 1976. — Zur phylogenetischen Stellung und Evolution der Cheliceraten. *Entomologica Germanica*, **3**: 1-12.

87. KRAUS, O., 1978. — *Liphistius* and the evolution of spider genitalia. *In:* P. MERRETT, *Arachnology. Seventh International Congress. Symposia of the Zoological Society of London. Number 42.* London, Academic Press: 235-254.

88. LAMEERE, A., 1932. — Les Arachnomorphes. *In:* A. LAMEERE, *Précis de Zoologie*, IV, 1. Bruxelles, Cauwenberg: 173-336.

89. LEGENDRE, R. & LOPEZ, A., 1981: Observations histologiques complémentaires chez l'araignée liphistiomorphe *Heptathela kimurai* Kishida, 1923 (Liphistiidae). *Atti della Società Toscana di Scienze Naturali, Mem., ser. B*, **88** suppl.: 34-44.

90. LEVI, H. W., 1982. — Uropygi. Schizomida. Ambylypgi. *In:* S. P. PARKER, *Synopsis and Classification of Living Organisms*. New York, Mac Graw Hill, **2**: 75-77.

91. LINDQUIST, E. E., 1984. — Current theories on the evolution of major groups of Arachnida with consequent implications for their classification. *In:* D. A. GRIFFITHS & C. E. BOWMAN, *Acarology VI. vol. 1.* Chichester, Ellis Horwood: 28-62.

92. LOPEZ, A. & BOISSIN, L., 1976. — La spermatide d'*Holocnemus pluchei* (Scop.) (Arachnida, Araneida, Pholcidae): Étude ultrastructurale. *Bulletin de la Société Zoologique de France*, **101**: 423-431.

93. LOPEZ, A., BONARIC, J.-C. & BOISSIN, L., 1983. — Étude ultrastructurale de la spermiogenèse chez l'araignée *Pisaura mirabilis* (Clerck, 1858) (Pisauridae). *Revue Arachnologique*, **5**: 55-64.

94. MANTON, S. M., 1938. — Studies on the Onychophora IV. The passage of spermatozoa into the ovary in *Peripatopsis*. *Philosophical Transactions of the Royal Society of London*, **228**: 421-442.

95. MICHAEL, A. D., 1892. — On the variation in the internal antomy of the Gamasinae, especially in that of the genital organs, and on their mode of coition. *Transaction of the Linnean Society of London (series 2)*, **5**: 281-324.

96. MILLOT, J., 1949. — Ordre Palpigrades. Ordre Uropyges. Ordre Amblypyges. *In:* P.-P. GRASSÉ, *Traité de Zoologie. VI.* Paris, Masson: 520-588.

97. MORITZ, M., 1993. — 1. Unterstamm Arachnata. *In:* H.-E. GRUNER, *Lehrbuch der Speziellen Zoologie (A. KAESTNER). Band I: Wirbellose Tiere.* Jena, G. Fischer: 64-442.

98. MOTHES, U. & SEITZ, K.-A., 1981. — The transformation of male sex cells of *Tetranychus urticae* (Acari: Tetranychidae) during passage from the testis to the oocytes: an electron microscopic study. *International Journal of Invertebrate Reproduction*, **4**: 81-94.

99. NORTON, R. A. & PALMER, S. C., 1991. — The distribution, mechanisms and evolutionary significance of parthenogenesis in oribatid mites. *In:* R. SCHUSTER & P. W. MURPHY, *The Acari. Reproduction, Development and Life-history Strategies*. London, Chapman & Hall: 107-136.

100. NORTON, R. A., KETHLEY, J. B., JOHNSTON, D. E. & OCONNOR, B. M., 1993. — Phylogenetic perspectives on genetic systems and reproductive modes of mites. *In:* D. WRENSCH & M. EBBERT, *Evolution and Diversity of Sex Ratio in Insects and Mites*. New York, Chapman & Hall: 8-99.

101. OLIVER, J. H. JR., 1982. — Tick reproduction: Sperm development and cytogenetics. *In:* F. D. OBENCHAIN & R. GALUN, *Physiology of Ticks*. Oxford, Pergamon Press: 245-275.

102. OLIVER, J. H. JR. & BRINTON, L. P., 1973. — Sperm maturation in ticks: an example of capacitation in invertebrates? *In:* M. DANIEL & B. ROSICKY, *Proceedings of the 3rd International congress of Acarology, Prague 1971*. The Hague, W. Junk: 733-737.

103. OSAKI, H., 1969. — Electron microscope study on the spermatozoon of the liphistiid spider, *Heptathela kimurai*. *Acta Arachnologica Tokyo*, **22**: 1-12.

104. OSAKI, H., 1972. — Electron microscope study on spermiogenesis in the spider, *Oxyopes sertatus*. *Japanese Journal of Zoology*, **16**: 184-199.

105. PETRUNKEVITCH, A., 1955. — Arachnida. *In:* R. C. MOORE, *Treatise on Invertebrate Paleontology. Part P. Arthropoda 2.* Lawrence, University of Kansas Press: P42-P162.

106. PHILLIPS, D. M., 1974. — Nuclear shaping in the absence of microtubules in scorpion spermatids. *Journal of Cell Biology*, **62**: 911-917.

107. PHILLIPS, D. M., 1976. — Nuclear shaping during spermiogenesis in the whip scorpion. *Journal of Ultrastructure Research*, **54**: 397-405.

108. RAY LANKASTER, E., 1904. The structure and classification of the Arthropoda. *Quarterly Journal of Microscopical Science*, **47**: 523-582.

109. REGER, J. F., 1970. — Spermiogenesis in the spider *Pisaurina* sp.: A fine structure study. *Journal of Morphology*, **130**: 421-434.

110. REMANE, A., 1962. — Arthropoda — Gliedertiere. *In:* L. V. BERTALANFFY & F. GESSNER, *Handbuch der Biologie. 6/1.* Konstanz, Akademische Verlagsgessellschaft Athenaion: 209-310.

111. REUTER, E., 1909. — Zur Phylogenie und Ontogenie der Acariden. Mit besonderer Berücksichtigung von Pediculopsis graminum (E. Reut.). *Acta Societatis Scientiarum Fennicae*, **36**: 1-281, pl.I-VI.

112. ROSATI, F., BACCETTI, B. & DALLAI, R., 1970. — The spermatozoa of Arthropoda. X. Araneids and the lowest myriapods. *In:* B. BACCETTI, *Comparative Spermatology*. New York, Academic Press: 247-254.

113. SAMSON, K., 1909. — Zur Spermiohistogenese der Zecken. *Sitzungsberichte der Gesellschaft naturforschender Freunde Berlin*, **8**: 486-499.

114. SAVORY, T. H., 1977. — *Arachnida*. London, Academic Press: 1-340.

115. SCHULT, J., 1983. — Taster haplogyner Spinnen unter phylogenetischem Aspekt (Arachnida: Araneae). *Verhandlungen des Naturwissenschaftlichen Vereins in Hamburg (NF)*, **26**: 69-84.

116. SCHULZE, P., 1937. — Trilobita, Xiphosura, Acarina. Eine morphologische Untersuchung über die Plangleichheit zwischen Trilobiten und Spinnentieren. *Zeitschrift für Morphologie und Ökologie der Tiere*, **32**: 181-223.

117. SHULTZ, J. W., 1990. — Evolutionary morphology and phylogeny of Arachnida. *Cladistics* **6**: 1-38.

118. STORCH, V. & RUHBERG, H., 1983. — Onychophora. *In:* K. G. ADIYODI & R. G. ADIYODI, *Reproductive Biology of the Invertebrates*. Chichester, John Wiley. **II**: 397-405.

119. STORCH, V. & RUHBERG, H., 1994. — Onychophora. *In:* F. A. HARRISON, *Microscopic Anatomy of Invertebrates. Vol. 12: Onychophora, Chilopoda, and Lesser Protostomia*. New York, Wiley-Liss: 11-56.

120. STÖRMER, L., 1955. — Chelicerata, Merostomata. *In:* R. C. MOORE, *Treatise on Invertebrate Paleontology. Part P. Arthropoda 2*. Lawrence, University of Kansas Press: 1-41..

121. SUHM, M. & ALBERTI, G., 1993. — The fine structure of the spermatheca of *Amaurobius fenestralis* (Stroem, 1768) (Amaurobiidae, Araneae). Proceedings of the XIV European Colloquium of Arachnology. *Bollettino dell'Accademia Gioenia di Scienze Naturali, Catania*.

122. SUHM, M., THALER, K. & ALBERTI, G. in press. — Investigations on the fine structure of glands in the male palpal organ and on the origin of the mating plug in the spiders *Amaurobius fenestralis* (Stroem, 1768) and *A. ferox* (Walckenaer, 1830) (Amaurobiidae, Araneae).

123. THOR, S., 1925. — Über die Phylogenie und Systematik der Acarina, mit Beiträgen zur ersten Entwicklungsgeschichte einzelner Gruppen. Teil 5-12. *Nytt Magasin foer Naturvidenskapene*, **63**: 260-313.

124. TILNEY, L. G., 1985. — The acrosomal reaction. *In:* C. B. METZ & A. MONROY, *Biology of Fertilization. 2. Biology of the Sperm*. Orlando, Academic Press: 157-213.

125. TRIPEPI, S., 1983. — Fine structure of spermiogenesis in *Phalangium opilio* L. (Opiliones, Phalangiidae). *Bulletin of the British Arachnological Society*, **6**: 109-114.

126. TRIPEPI, S. & SAITA, A., 1985. — Ultrastructural analysis of spermiogenesis in *Admetus pomilio* (Arachnida, Amblypygi). *Journal of Morphology*, **184**: 111-120.

127. TOKUYASU, K. T., 1974. — Dynamics of spermiogenesis in *Drosophila melanogaster*. IV. Nuclear transformation. *Journal of Ultrastructure Research*, **48**: 284-303.

128. UHL, G., 1994. — General morphology and sperm storage in *Pholcus phalangioides* (Fuesslin, 1775) (Pholcidae; Araneae). *Acta Zoologica (Stockholm)*, **75**: 1-12.

129. VITZTHUM, H. GRAF VON., 1940/43. — Acarina. *In: Bronns Klassen und Ordnungen des Tierreichs*. Leipzig, Akademische Verlagsgesellschaft. 5, IV, 5: 1-1011.

130. VOGLMAYR, J. K., 1987. — Surface protein changes in ram spermatozoa during maturation and capacitation. *In:* H. MOHRI, *New Horizons in Sperm Cell Research*. Tokyo, Japan Scientific Societies Press: 3-18.

131. WAGNER-JEVSEENKO, O., 1958. — Fortpflanzung bei *Ornithodorus moubata* und genitale Übertragung von *Borrelia duttoni*. *Acta Tropica*, **15**: 119-168.

132. WERNER, F., 1935. — Scorpiones, Pedipalpi. *In: Bronns Klassen und Ordnungen des Tierreichs*. Leipzig, Akademische Verlagsgesellschaft. 5, IV, 8: 1-490.

133. WERNER, G. & BAWA, S. R., 1988a. — Acrosome formation in the pseudoscorpion *Diplotemnus* sp. *Journal of Ultrastructure and Molecular Structure Research*, **98**: 105-118.

134. WERNER, G. & BAWA, S. R., 1988b. — Spermatogenesis in the Pseudoscorpion *Diplotemnus* sp. with special reference to nuclear changes. *Journal of Ultrastructure and Molecular Structure Research*, **98**: 119-136.

135. WERNER, G. & BAWA, S. R., 1988c. — Mitochondrial changes in spermatogenesis of the pseudoscorpion, *Diplotemnus* sp. *Journal of Ultrastructure and Molecular Structure Research*, **98**: 281-293.

136. WEYGOLDT, P. & PAULUS, H. F., 1979a. — Untersuchungen zur Morphologie, Taxonomie und Phylogenie der Chelicerata. I. Morphologische Untersuchungen. *Zeitschrift für zoologische Systematik und Evolutionsforschung*, **17**: 85-116.

137. WEYGOLDT, P. & PAULUS, H. F., 1979b. — Untersuchungen zur Morphologie, Taxonomie und Phylogenie der Chelicerata. II. Cladogramme und die Entfaltung der Chelicerata. *Zeitschrift für zoologische Systematik und Evolutionsforschung*, **17**: 177-200.

138. WIRTH, U., 1984. — Die Struktur der Metazoen-Spermien und ihre Bedeutung für die Phylogenetik. *Verhandlungen des Naturwissenschaftlichen Vereins in Hamburg (NF)*, **27**: 295-362.

139. WITALINSKI, W., 1975. — Spermatogenesis in free living mite, *Pergamasus viator* Halas (Parasitidae, Mesostigmata). I. Fine structure of spermatozoa. *Zeitschrift für mikroskopisch-anatomische Forschung*, **89**: 1-17.

140. WITALINSKI, W., 1976. — Spermatogenesis in free living mite, *Pergamasus viator* Halas (Parasitidae, Mesostigmata). II. Spermiogenesis. *Zeitschrift für mikroskopisch-anatatomische Forschung*, **90**: 657-680.

141. WITALINSKI, W., 1979. — Fine structure of the spermatozoon in the mite *Parasitus niveus* (Mesostigmata, Acari). *International Journal of Invertebrate Reproduction*, **1**: 141-149.

142. WITALINSKI, W., 1982. — Spermiogenesis and structure of spermatozoa in the oribatid mite, *Hafenrefferia gilvipes* (C. L. Koch) (Acari, Oribatida). *International Journal of Invertebrate Reproduction*, **5**: 43-56.

143. WITALINSKI, W. & DALLAI, R., 1993. — F-actin and tubulin during spermatogenesis in gamasid mites (Acari: Parasitina). *Acta Zoologica (Stockholm)*, **74**: 205-214.

144. WITALINSKI, W., JONCZY, J. & GODULA, J., 1986. — Spermatogenesis and sperm structure before and after insemination in two acarid mites, *Acarus siro* L. and *Tyrophagus putrescentiae* (Schrank) (Acari, Astigmata). *Acarologia*, **27**: 41-51.

145. WITALINSKI, W., SZLENDAK, E. & BOCZEK, J., 1990. — Anatomy and ultrastructure of the reproductive systems of *Acarus siro* (Acari: Acaridae). *Experimental & Applied Acarology*, **10**: 1-31.

146. WITTE, H., 1991. — Indirect sperm transfer in prostigmatic mites from a phylogenetic viewpoint. *In:* R. SCHUSTER & P. W. MURPHY, *The Acari. Reproduction, Development and Life-history Strategies*. London, Chapman & Hall: 137-176.

147. YAMAMICHI, Y. & SEKIGUCHI, K., 1982. — Axoneme patterns of spermatozoa of Asian horseshoe crabs. *Experientia*, **38**: 1219-1220.

148. YOSHIKURA, M., 1975. — Comparative embryology and phylogeny of Arachnida. *Kumamoto Journal of Science, Biology*, **12**, 71-142.

149. ZACHVATKIN, A. A., 1945. — On the discovery of Palaeacariformes in the U.S.S.R. *Comptes Rendus de l'Académie des Sciences de l'URSS, Moscou, n.s.*, **47**: 673-676.

150. ZACHVATKIN, A. A., 1952. — Division of the Acarina into orders and their position in the system of the Chelicerata. *Magasin de Parasitologie de l'Institut de Zoologie de l'Académie des Sciences de l'URSS, Moscou*, **14**: 5-46.